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Social Organization of Tigers (*Panthera tigris*) in Royal Chitawan National Park, Nepal

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The Social Organization of Tigers (*Panthera tigris*) in Royal Chitawan National Park, Nepal

Melvin E. Sunquist

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ABSTRACT

Sunquist, Melvin E. The Social Organization of Tigers (*Panthera tigris*) in Royal Chitawan National Park, Nepal. *Smithsonian Contributions to Zoology*, number 336, 98 pages, frontispiece, 33 figures, 31 tables, 1981.—The movements and social-spatial system of tigers were studied using radiotelemetry. A total of seven tigers was radio-tracked for varying periods from December 1974 to September 1976. Population characteristics are described and examined in relation to information from other studies. Seasonal activity patterns and habitat use of tigers are detailed and evaluated with regard to several environmental parameters. Daily and seasonal movements of animals are emphasized and discussed in relation to foraging, reproductive activity, and territoriality. Estimates of the extent to which tigers of various sex and age classes socialize, and the circumstances under which they do so, are presented and considered with respect to factors promoting and maintaining a solitary and dispersed social system. Various aspects of the feeding ecology of tigers are detailed and incorporated into an assessment of the impact of predation on prey populations. Results from this study are then viewed in an evolutionary perspective in comparison with the lion (*Panthera leo*).

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The Social Organization of Tigers (*Panthera tigris*) in Royal Chitawan National Park, Nepal

Melvin E. Sunquist

Introduction

Few animals evoke such strong feelings of fear and awe as the tiger. For centuries its behavior has inspired legends, and great metaphysical powers have been attributed to its bones, claws, and whiskers. The tiger's ability and occasional proclivity for killing man has only intensified its mystique. Despite the animal's broad geographical distribution and its apparent adaptability to a wide variety of environmental conditions, it has only recently been the subject of scientific investigation. Schaller's (1967) study of the tiger and its prey in Kanha Park, India, provided the first insights into the ecology and behavior of this species. More recently, McDougal's (1977) observations on the behavioral ecology of tigers in Chitawan National Park, Nepal, has expanded the data base. The tiger has received little attention in other parts of its range except for the work of Russian scientists (Matjushkin, et al., 1977). Other relevant information on this species has been summarized by Perry (1964) and Mazak (1965).

The tiger is the largest of all living felids. Like others in the genus *Panthera*, its morphology reflects adaptations for the capture and killing of large and potentially dangerous prey, by concealment, stealth, and sudden attack. Indeed, none of the large cats, excluding the cheetah (*Acinonyx jubatus*), overcome prey by long chases. The evolution of specialized hunting techniques that require crypticity for success, and the maintenance of an almost exclusive animal diet also appears to have favored a solitary existence (Kleiman and Eisenberg, 1973). Correspondingly, most adult felids, with the exception of the social lion, are intolerant towards adults of the same sex and commonly exhibit a spatially or temporally dispersed social system. While tigers and possibly other *Panthera* could be as social as the lion, by virtue of their morphological similarities (Hemmer, 1978b; Fisler, 1969; Eisenberg, 1966), the exigencies of the closed habitats in which they live have apparently not fostered the development of complex social structures (Kleiman and Eisenberg, 1973).

The large, solitary felids do, however, have rich communication repertoires and viable communal lives (Leyhausen, 1965; Peters, 1978). Unfortunately, our understanding of their social systems, and how these differ in response to varying environmental conditions is limited due to their secre-

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tive nature, nocturnal habits, and wide ranging movements. The most intensively studied of the large, solitary cats is the mountain lion (*Felis concolor*) (Hornocker, 1969, 1970; Seidensticker, et al., 1973). Leopards (*Panthera pardus*) have been studied in several African parks (Schaller, 1972; Grobler and Wilson, 1972; Hamilton, 1976; R. M. Smith, 1978) and in Sri Lanka (Eisenberg and Lockhart, 1972; Muckenhirn and Eisenberg, 1973); but the jaguar (*Panthera onca*) and snow leopard (*Panthera uncia*) have received little attention.

Against this background, my study in Chitawan National Park, Nepal, was designed to investigate in more detail the relationship between the ecology and social-spatial system of the tiger by incorporating radiotelemetry. I was interested primarily in movements and spacing patterns as these are expected to closely reflect the tiger's response to environmental features, including conspecifics. Specifically, I wanted to examine: (1) In what way do individuals utilize their home range space with regard to resources?, (2) What are the patterns of movement exhibited by individuals relative to each other?, (3) What mechanisms are involved in spacing behavior?, and (4) What factors may predispose or constrain individuals to particular patterns of spacing behavior? To gain further insight into this population's resource requirements data were also collected on feeding ecology.

Whether results from this study are applicable to other areas awaits confirmation; indeed, even in Chitawan conditions may change that would result in an altered social system. Any short-term study of a long-lived animal is only a glimpse, and the utility of such a study is only increased when more than a single-species or a single population approach is taken. Fortunately my study was part of an ongoing project designed to provide a comprehensive understanding of the tiger in its natural habitat.

The need for ecological and behavioral research on the tiger and its prey was recognized by His Majesty's Government of Nepal (HMG), and as a result a cooperative agreement between HMG and the Smithsonian Institution was established in 1973 for the initiation of a long-term research project in Chitawan National Park. Supported by grants from the Smithsonian Institution and World Wildlife Fund (U.S. Appeal), field work began in November 1973. Chitawan was selected because tigers and ungulates are fairly abundant, poaching and grazing of livestock are controlled by guards, and the area is relatively undisturbed.

Research efforts in Chitawan have proceeded on an integrative and expanding basis. J. Seidensticker and K. M. Tamang developed capture and immobilization techniques (Seidensticker, et al., 1974), and began radiotagging tigers and other large mammals. Preliminary data on tiger home range patterns, movements, and tiger-leopard niche separation were obtained by Seidensticker (1976a). Early maternal behavior of the leopard was examined by Seidensticker (1977). He also obtained preliminary estimates of ungulate density and biomass (Seidensticker, 1976b). Tamang studied the population characteristics of the prey species and the impact of predation on prey populations from 1973–1977. I joined the project in late 1974 and investigated movements and social-spatial patterns of tigers until August 1976. Since January 1977, J.L.D. Smith has focused on dispersal of tigers and completed his studies in 1980. In 1978 H. R. Mishra began a study of the population dynamics and behavior of chital (*Axis axis*), an important prey species of the tiger.

During the same time period several complementary studies have been conducted in Chitawan. A brief botanical survey was undertaken by R. G. Troth and D. H. Nicolson (1977); W. A. Laurie (1978) completed a detailed study of the ecology and social organization of the greater one-horned rhinoceros (*Rhinoceros unicornis*); and the behavioral ecology of the sloth bear (*Melursus ursinus*) was investigated by Laurie and Seidensticker (1977).

ACKNOWLEDGMENTS.—This study would not have been possible without the help of several organizations and numerous individuals to whom I wish to express my sincere thanks.

Generous financial support for the project was provided throughout its entirety by the Smithsonian Institution and the World Wildlife Fund (U.S. Appeals). I would also like to acknowledge the interest and support of Dr. S. D. Ripley, Secretary of the Smithsonian Institution; Dr. D. Challinor, Assistant Secretary for Science, Smithsonian Institution; and Mr. Ross Simons, Project Administrator, Smithsonian Institution. Without their contribution the work could not have been completed.

The ongoing investigation of the tiger and its prey in Royal Chitawan National Park, Nepal, has been a cooperative effort between the Smithsonian Institution and the National Parks and Wildlife Conservation Department (NPWCD), His Majesty's Government of Nepal (HMG). The enthusiasm and support of government officials during the study are greatly appreciated, and many people in Nepal were very cooperative and helpful in all phases of the project. A few of the individuals who gave so generously of their time and skills include Mr. A. R. Rajbhandari, Secretary, Ministry of Forests (HMG), and former Secretary, Mr. T. B. Rayamajhi; Mr. Emerald J. B. Rana, Chief Conservator of Forests, Department of Forests (HMG); Mr. B. N. Upreti, Chief, National Parks and Wildlife Conservation Department (HMG), and former Chiefs, Mr. B. B. Shah, and Mr. P.B.S. Pradhan; Mr. Hemanta R. Mishra, Ecologist (NPWCD); Mr. J. K. Tamrakar, former Warden, Royal Chitawan National Park, and Warden, Mr. T. M. Maskey. The generosity, hospitality, and friendship of Hemanta Mishra and Sushama Mishra are greatly appreciated. The cooperation and assistance of Frank Poppleton, Foreign Agriculture Office (FAO) Wildlife Advisor to Nepal; Major Chetri, FAO Project Administrator, and FAO ecologists Melvin Bolton and Per Wegge are gratefully acknowledged. Andrew Laurie and Ranald Laurie provided me with information on tagged animals and occasional company in the field. Rebecca Troth also contributed her delightful company, plus important botanical information. Many Peace Corps volunteers helped me on several occasions, including data collection, and I would like to thank Will Weber, Luke Golobitsh, John Lehmkuhl, Paul Wilson, Eric Dinerstein, Tom Dahmer, Cathy Johnson, and Cliff Rice. I am grateful also to Dieter Plage for flying me over the study area on several occasions.

In particular, I wish to thank Kirti Man Tamang, co-principal investigator on the project, B. L. Tharu, Bhadai Tharu, and all other shikari and elephant staff at the camp for their contribution in making this study a memorable experience. P. B. Yonzon and S. P. Timilsina, project assistants, did a remarkable job, especially during the period of K. M. Tamang's recovery from being mauled by a tigress. I would especially like to thank P. B. Rai, Subedar of Shikaris, for allowing me to witness and partake in his understanding of tracks and signs.

Through numerous discussions with James L. D. Smith, Charles McDougal, and John Seidensticker, my understanding of tigers in Chitawan, and of Chitawan itself, has been greatly enhanced. All have contributed in many other ways as well, particularly Smith, who not only helped in the capture, tagging, and radio-tracking of several tigers in 1976, kept me up-to-date on the whereabouts and activities of known and new tigers in the park, but magnanimously allowed me to incorporate some of his unpublished data into this paper. I sincerely thank these people for their help and cooperation.

I would also like to thank my academic advisor, Dr. D. B. Siniff, for his understanding and assistance throughout all aspects of the project. Drs. D. B. Siniff, P. A. Jordan, M. Weller, E. Birney, and H. Tordoff provided helpful comments, criticisms, and suggestions on an earlier draft of this paper. A special thanks to R. Rice and D. Stinson for typing the earlier draft and to J. Wendt for all the many ways in which she helped. The computer analysis was done only with the cooperation and patience of K. Zinnel. The additional help, encouragement, and company of Francie Cuthbert are greatly appreciated.

Write-up support for this paper was provided through the Department of Zoological Research, National Zoological Park, Smithsonian Institution. I would especially like to thank the staff at the Conservation and Research Center for all their help and cooperation. Sigrid James Bruch prepared the figures and Virginia Garber typed the manuscript; their efforts are greatly appreciated. A special thanks to Betty Howser and Gail Hill for handling the administrative details. The development of this paper has benefitted significantly from discussions with and reviews by numerous people associated with the National Zoo. The advice, criticism, and editorial suggestions of John Eisenberg, Devra Kleiman, Chris Wemmer, John Seidensticker, Joel Berger, Jon Rood, Hazel Rood, Maxeen Biben, Jack Frazier, James Malcolm, Kathy Ralls, and Rauf Ali were invaluable. I am grateful for having had the opportunity to interact with these individuals. In addition, the generosity, encouragement, concern, and support of John Eisenberg and Devra Kleiman are deeply appreciated.

The greatest contributor to this work has been my wife, Fiona, who willingly helped out in the field and participated in virtually every aspect of the study, from the initial capture of animals, data collection and analysis, to writing and typing of the manuscript. She also took the photographs used in this paper. Her enthusiasm for the project and for a relatively primitive life in the field contributed in an important way to the progress of the study.

Study Area

Royal Chitawan National Park lies in the Rapti Valley in the Chitawan District at approximately 27°30′N latitude and 84°20′E longitude (Figure 1). The valley is bounded on the north by the Mahabharat Lekh (outer Himalayan range) and on the south by the low-lying Churia and Someswar Hills, collectively known as the Siwaliks. The Siwalik Range runs in a line roughly parallel to the Indian border and in places the range divides, forming interior valleys known as "duns." The Rapti Valley is a "dun" valley.

The park covers an area of 544 km^2 (210 mi^2) and is situated between the Rapti River, which forms the northern boundary, and the Reu River, which forms most of the southern boundary. The southwestern boundary follows the international border of Nepal and India for a short distance and then extends northwards along the Narayani River, which forms the western boundary. In all, more than half of the park boundary is delimited by rivers. In 1977, after this study was terminated, the park was expanded to about 932 km^2 (360 mi^2).

HISTORICAL DEVELOPMENT OF ROYAL CHITAWAN NATIONAL PARK

Until 1950 Chitawan and the adjoining forest areas in central Nepal remained unsettled except for a few scattered villages of the indigenous Tharus. The presence of malaria, and a government policy discouraging settlement and clearing afforded protection to the area (Rose, 1971; Burkhill, in Stainton, 1972). In addition, the entire Chitawan District (over 2600 km^2) was the private preserve of the privileged classes; Chitawan was well-known for its abundance and variety of wild game (Smythies, 1942). Hunting of tiger, rhino, leopard, and bear was conducted on a lavish scale for kings and foreign dignitaries and employed hundreds of elephants and beaters to drive and encircle the game. Hunts were held at irregular intervals and limited to the cool months of December through February. According to Smythies (1942): during a shoot organized for King George V of England in 1911, 39 tiger, 18 rhino, and 4 bear were taken in 11 days. In 1921 the Prince of Wales and his party shot 17 tigers, 10 rhinos, 2 leopards, and 2 bears. A total of 41 tigers and 2 leopards was shot during a 20-day hunt in 1923. The last tiger hunt was in 1938–1939, extended over the entire Chitawan District, and produced a bag of 120 tigers, 27 leopards, and 15 bears.

In the 1950s, with the pressing need for new agricultural land, the Chitawan District was opened for settlement and people from northern Nepal migrated there and began clearing the forest for cultivation. However, the presence of malaria was a serious deterrant to settlement. A

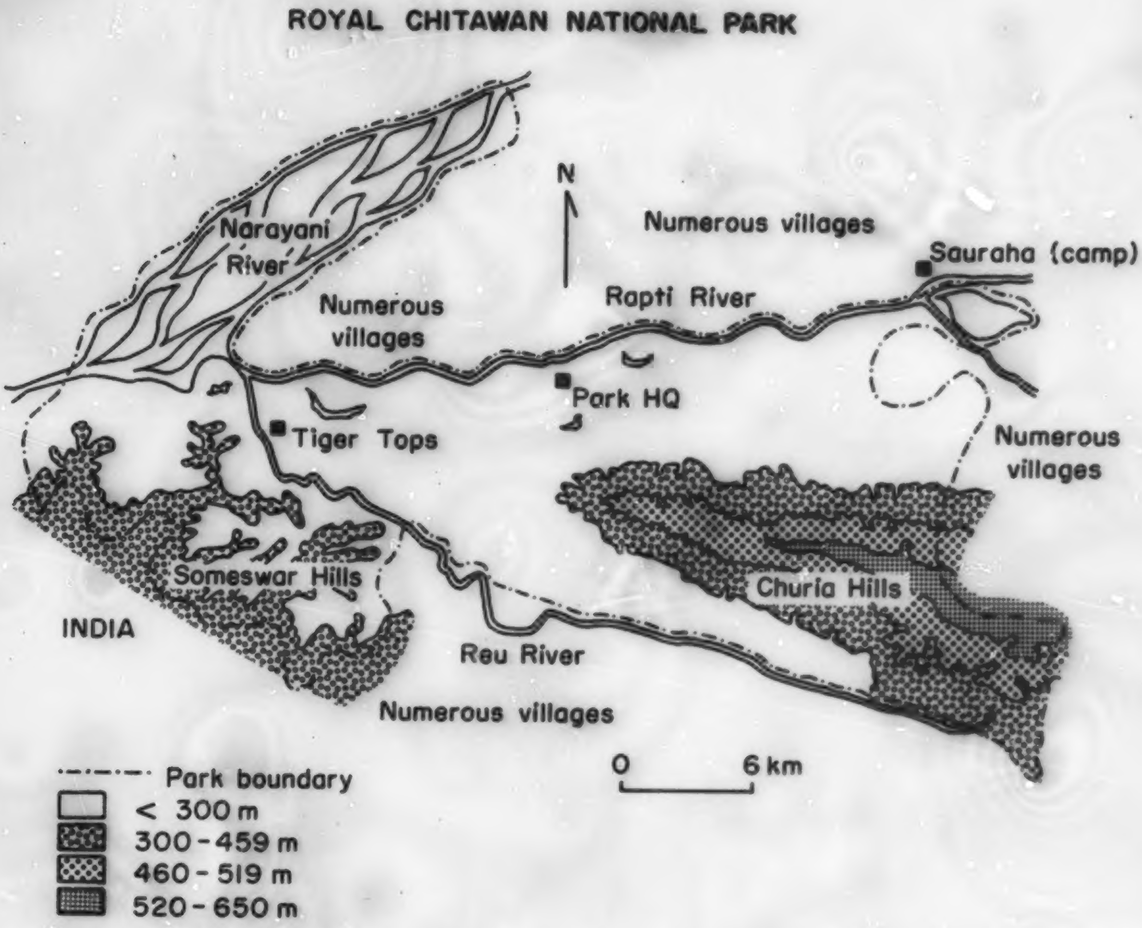
ROYAL CHITAWAN NATIONAL PARK
N
Numerous villages
Sauraha (camp)
Narayani River
Numerous villages
Rapti River
Park HQ
Tiger Tops
Numerous villages
Someswar Hills
INDIA
Churia Hills
Reu River
Numerous villages
0
6 km
Park boundary
< 300 m
300-459 m
460-519 m
520-650 m

FIGURE 1.—Location, setting, and topographic features of Royal Chitawan National Park, Nepal.

malaria eradication program began in 1954, and by 1960 the entire Chitawan area was declared malaria free. This, combined with the construction of roads, accelerated the influx, and by the early 1960s over two-thirds of the forest and grassland north of the Rapti River had been put into cultivation (McDougal, 1977). The destruction of wildlife habitat by the activities of an estimated 100,000 people became a serious problem (Willan, 1965), and His Majesty's Government of Nepal, at the recommendation of the Fauna Preservation Society, created (1961-1962) Mahendra Park north of the Rapti River and a rhino sanctuary south of the river (Gee, 1959, 1963; Willan, 1965).

In 1963 a government committee was established to examine the legal status of settlers in Chitawan. This was followed in 1964 by the creation of a Land Settlement Commission, which was empowered to remove illegal squatters and resettle them in other areas in the Rapti Valley (Willan, 1965). As a result, some 22,000 people were removed, including 4000 who had settled in the rhino sanctuary. However, grazing and the collection of forest products were still allowed within the sanctuary under permits issued by the Forest Department.

In 1970 the King of Nepal approved the establishment of a national park south of the Rapti River. This area included the rhino sanctuary. Preliminary development began in 1971 and in 1973 Royal Chitawan National Park was legally established.

At present, the park is administered by the National Parks and Wildlife Conservation Department (NPWCD). There is a Park Warden, responsible to NPWCD, and over 100 military guards stationed throughout the park at outposts called "chowkis." The guards are under a commanding officer, who serves as a liaison between the Army and the NPWCD.

CLIMATE

There are three climatic seasons. A cool period extends from October to late February, during which winds are northerly, maximum daytime temperature average about 25°C (Figure 2), nights are cool and damp with relative humidity approaching 100%, resulting in heavy ground fog and dew-soaked vegetation. Occasional frosts have been recorded in December and January (His Majesty's Government of Nepal, 1970). Very little precipitation in the form of rain falls during this period.

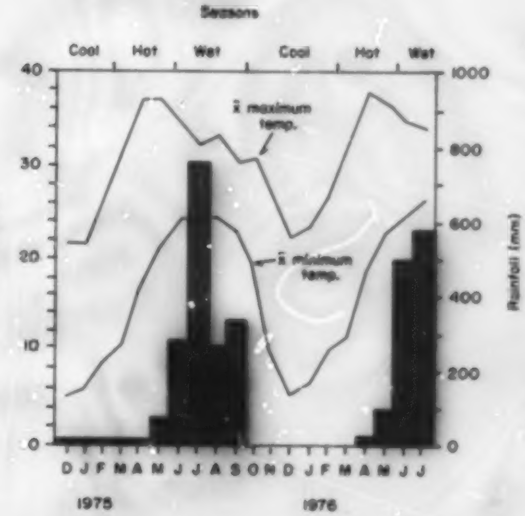

FIGURE 2.—Mean maximum and minimum monthly temperature and rainfall at Sauraha (camp) during study period.

A hot season extends from March to late May, during which winds are southwesterly, maximum daytime temperatures average 36°C, and relative humidity is at its lowest level. Sporadic violent storms with strong winds, blowing sand, hail, and rain occur with increasing frequency from late March to May. Towards the end of May intense afternoon showers become common, signaling the forthcoming monsoon.

A wet period extends from June through September, during which winds are southeasterly, maximum daytime temperatures average 33°C and minima are seldom below 24°C, relative humidity is very high, and rainfall is frequent. The total rainfall at Sauraha (Tiger Ecology Project Headquarters) in 1975 was 176.5 cm, 98% of which fell between May and September. Laurie (1978) recorded an annual average rainfall of 242 cm at Sauraha for 1973–1975, 92% of which fell from May through September. By comparison, at the Rapti Agricultural Station, about 16 km west of Sauraha, the annual average rainfall for 1958–1966 was 215.6 cm and 93% of that fell from May through September (His Majesty's Government of Nepal, 1970).

TOPOGRAPHY

The general topography of the park is shown in Figure 1. The floodplain south of the Rapti River extends for about 40 km from Sauraha westward to the Narayani River and varies in width from 1.6 to 4.8 km. The altitude on the floodplain is about 150 m (above sea level) and rises to about 650 m on the crest of the Churia Hills. Except for a narrow ridge which rises to about 520 m, the Someswar Hills within the park lie below 450 m.

DRAINAGE AND HYDROBIOLOGICAL REGIME

From the watersheds of the Churia Hills numerous permanent and seasonal streams flow northwards into the Rapti River and southwards into the Reu River. Both the Rapti and Reu Rivers flow westward and become confluent before joining the Narayani River. Drainage in the park is generally good and permanent standing water is almost entirely confined to small lakes ("tals"), which are scattered throughout the park. The Rapti and Reu Rivers are at their lowest level in the hot season and at this time are easily crossed on foot. During the wet season, however, water levels in the rivers will rise 2–3 m or more and extensive areas of the floodplains become waterlogged or inundated for 1–2 weeks at a time. During peak flows the rivers are impassable.

GEOLOGY AND SOILS

The bedrock is late Tertiary Siwalik formation, composed of sandstone, conglomerates, shales, and micaceous sandstone (His Majesty's Government of Nepal, 1968). The alluvial river plains are recent, and consist of deep, sandy loams or eroded gravelly loams that are dark in color. Outcrops of parent material are evident in steep terrain.

VEGETATION

Chitawan Park has three basic vegetation types: sal forest (70%), riverine forest (7%), and grassland (20%). The remaining area is primarily open river bank (Figure 3).

SAL FOREST.—Upland sites (Figure 4) support

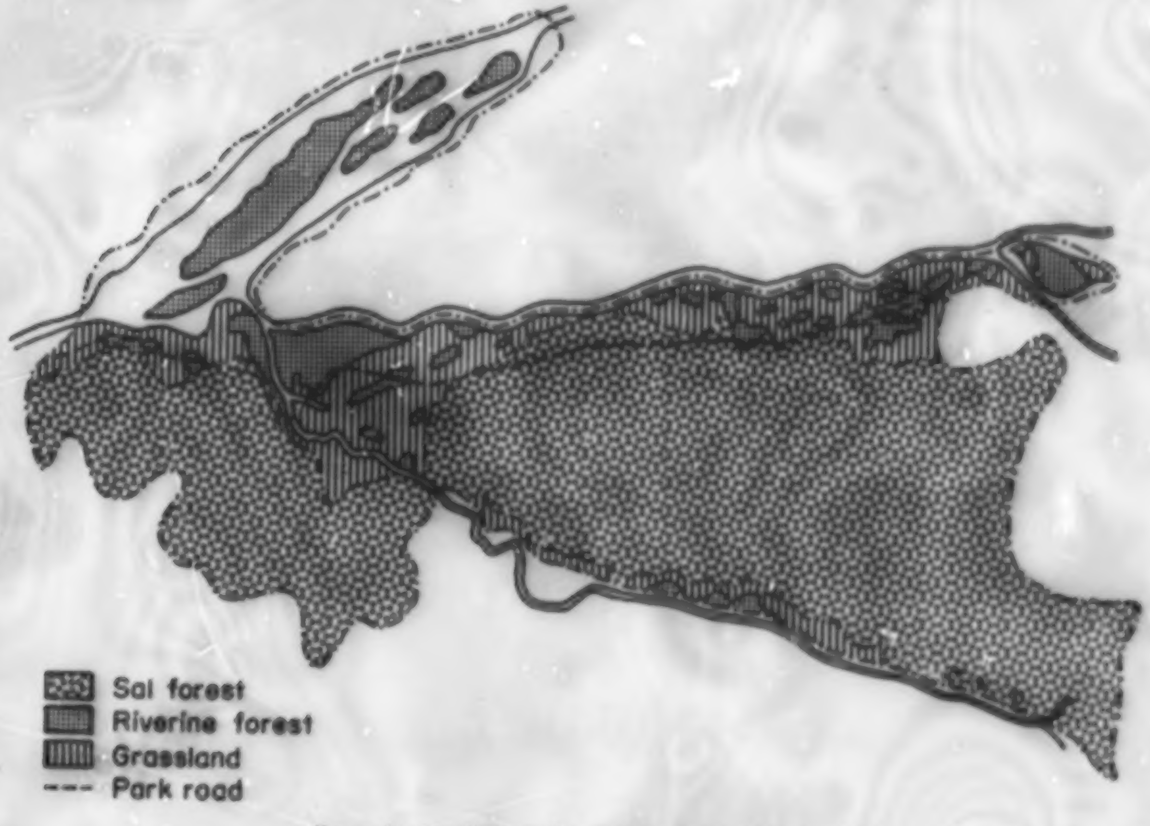

FIGURE 3.—Distribution of vegetation types in Chitawan Park.

BEST DOCUMENT AVAILABLE

FIGURE 4.—Sal forest predominates on well-drained upland sites in park.

sal (*Shorea robusta*), a climax form of moist deciduous forest (Champion and Seth, 1968). Sal trees do not grow on recently formed alluvium or poorly drained soils (Stainton, 1972). Sal frequently grows in monotypic stands, attains heights of 20–25 m, and a shrub layer is usually absent, giving the impression of an open woodland. Beneath the sal forest grasses such as *Narenga porphyrocoma* and *Thyrsia zea* attain heights of 1 m in some areas, and in clearings Narenga forms dense stands 4–6 m in height. In the few areas where the canopy is continuous the ground is often bare except for leaf litter and an occasional tuft of grass. Palms occur on the upper, drier ridges of the Churia and Someswar Hills where the understory is very light. Sal interspersed with pine (*Pinus roxburghii*) occurs on the ridges in the eastern part of the park. Bamboo species are found on the moist northern slopes of the valleys and ravines of the Siwaliks.

RIVERINE FOREST.—Riverine forest occurs along streams, lakes, and rivers in the park, and it is quite variable in composition and form (Figure 5). Khair (*Acacia catechu*) and sisso (*Dalbergia sisso*) dominate the banks of the Rapti and Narayani Rivers on recent alluvium and on gravel islands in the middle of the watercourses. Khair, a moderately large thorn tree, may be found away from water, but sisso is unlikely to be found outside of riverine situations. One of the two species may be dominant in an area but there is commonly a dense shrub understory of *Pogostomon plectranthoides*, plus a variety of shade-tolerant herbs and grasses. Dense beds of tall (3–4 m) grass (*Saccharum* species) frequently occur along the forest-floodplain interface.

The Khair-sisso association is a colonizing vegetation type that stabilizes soil on the riverside terraces, and other tree species, particularly simal (*Bombax ceiba*) and *Trewia nudiflora*, later appear (Stainton, 1972). This association rarely forms a continuous canopy and a dense shrub layer, dominated by *Colebrookea oppositifolia*, *Clerodendrum infortunatum*, and *Callicarpa macrophylla*, occurs where the canopy is broken (Troth and Nicolson, 1977).

Riverine forest does not form a continuous belt along rivers and streams, but more commonly appears as a mosaic of patches surrounded by grassland or intermixed with grasslands to form dense shrub thickets. Savanna conditions prevail where simal has invaded the grasslands (Figure 6).

GRASSLAND.—A diverse and complex assemblage of grasses are found in the park; over 40 species are reported from just near Sauraha alone (Laurie, 1978). Luxuriant grasslands are a prominent feature of the alluvial plains, and an event common to all grasslands on low-lying areas is periodic inundation during the monsoon season. Some grasslands are rather short-lived, becoming established on exposed silt beds as the river level falls during the monsoon, and then disappearing as the water level rises. Species commonly found in this situation include *Cynodon dactylon*, *Eragrostis japonica*, *Brachiaria ramosa*, and *Andropogon* species (Laurie, 1978). *Saccharum spontaneum* is one of the first species to invade newly formed floodplains and may form pure stands that reach a height of 2 m; it is replaced by *Narenga* species or other *Saccharum* species if repeatedly burned (Bor, 1960). Along streams and around lakes, tall (3–5 m), dense stands of coarse grasses, such as *Themeda*

FIGURE 5.—Patches of riverine forest mixed with grassland on floodplain in park.

FIGURE 6.—Savanna conditions on floodplain in park, with sal forest on slopes of Churia Hills in background.

villosa, *Saccharum ravennae*, and *Arundo donax*, are commonly found. On moist areas away from the watercourses and extending into the savannas are extensive, dense stands of *Saccharum procerum*, *Phragmites karka*, *Arundinella nepalensis*, and *Themeda arundinacea*. Some of these grasses attain heights of 7–8 m, the tallest measured was 7 m, but 4–6 m is common (Figure 7). Shorter (1–3 m) grasses, such as *Imperata cylindrica* (thatching grass), *Bothriochloa intermedia*, and taller *Saccharum* species predominate on old village sites, thus adding to the overall complexity of the grasslands.

HUMAN ACTIVITIES IN CHITAWAN PARK

Numerous villages and hamlets are located along the north (Figure 8), northeast, and southeast boundaries of the park (Figure 1). Although it is illegal, villagers collect firewood, fruits, tubers, fodder for livestock, and building materials from the park. Village livestock are grazed, accidentally and deliberately, within the park. Cattle caught in the park are impounded and a fine is levied for release. In 1974 an estimated 6458 cattle were impounded (Nepal Nature Conservation Society Report, 1975), some of which were probably impounded several times. However, it is doubtful that all livestock entering the park are caught. The impact of the foraging and grazing activities of villagers and their livestock on the vegetation is unknown, but it certainly is much less than that observed on forest areas outside the park. According to Laurie (1978), at least 10 shrub species disappeared over a 3-year period from a small area of riverine forest just outside the park; this loss of species was directly attrib-

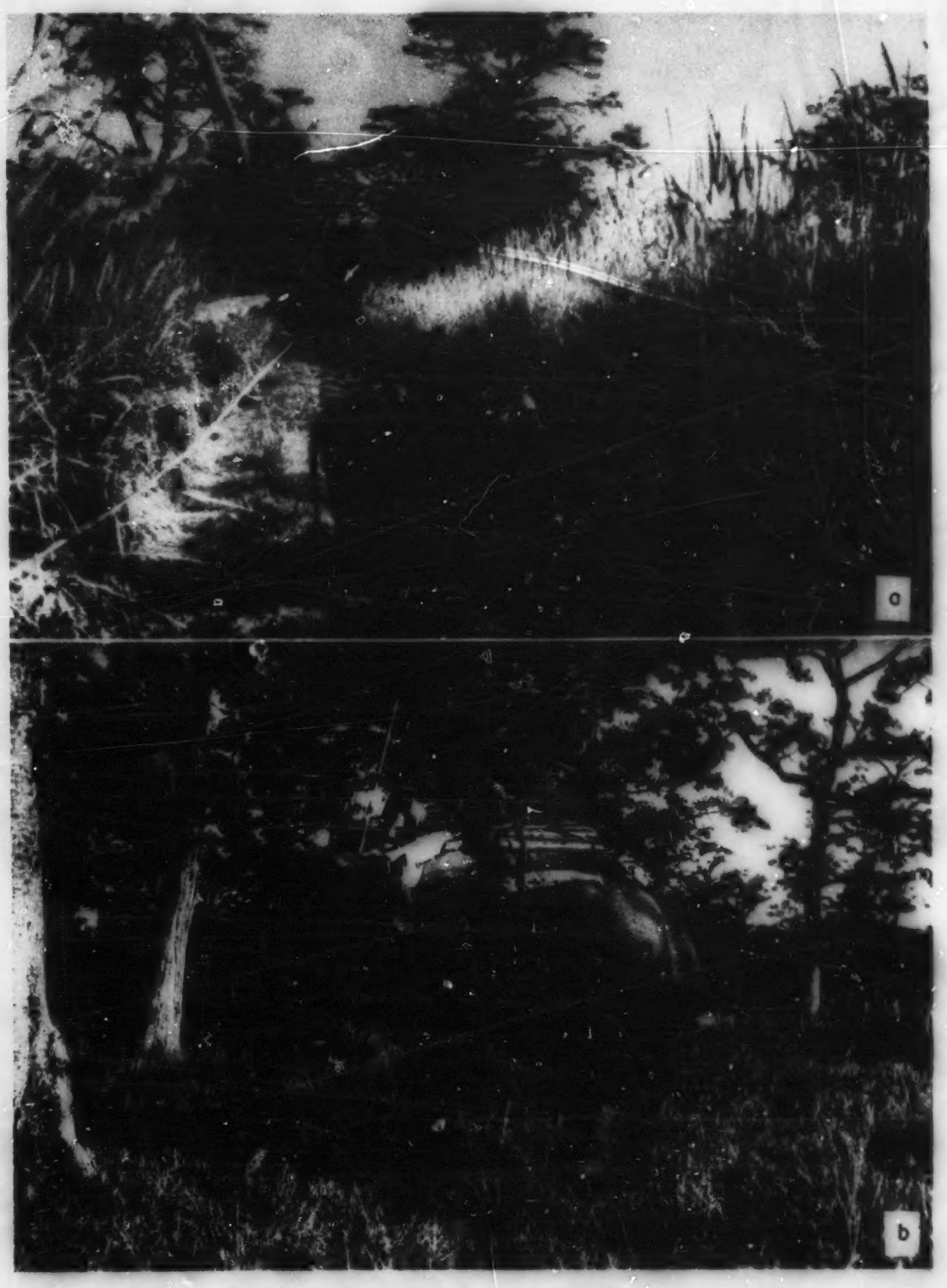

FIGURE 7.—Mixture of (*a*) tall and (*b*) short grasses prominent on floodplain in park.

FIGURE 8.—Numerous villages located along northern boundary of park (oxbow lakes indicate former river courses; Mahabharat Lekh (outer Himalayan Range) visible in background).

utable to the foraging activities of villagers and their livestock. The result has been an unhindered spread of unpalatable species, particularly thorny shrubs such as *Zizyphus mauritania*. A similar observation was reported by Schaller (1967) for Kanha Park in north-central India.

Villagers are allowed in the park during the month of January each year to cut grass (Figure 9). While cutting is ostensibly restricted to thatch grass (*Imperata cylindrica*), villagers also burn and cut the tall-grass species (e.g. *Saccharum ravennae* and *Themeda arundinacea*). Burning removes the dead outer layers of the grass, leaving the thick, cane-like inner stalks that are then cut and used for the construction of walls. Though illegal, the burning of grasslands continues into February and March and only those areas on moist sites tend to remain unburned. Fires burn unchecked and spread into the riverine and sal forests. Burning in the sal forests continues during April and lines of fire are commonly seen on the hills at night. Historically, grasslands and forests in this part of the world have been burned annually for probably 2000 years (Wharton, 1968).

FAUNA

While Nepal lies in the zone of overlap between the southern Oriental fauna and the northern Paleartic fauna, the terrestrial mammalian species in Chitawan are typically those found in peninsular India (Prater, 1971). Table 1 lists the large mammals presently found in Chitawan Park.

Wild Asiatic elephant (*Elephas maximus*) formerly occurred in Chitawan (Spillett and Tamang, 1966), and Swamp deer (*Cervus duvanceli*) were present in marshy areas north of the Rapti River until the late 1950s, and then disappeared as these areas came under cultivation (K. M. Tamang, pers. comm.). Wild water buffalo (*Bubalus bubalis*) were also present (Smythies, 1942), but no account details their disappearance. Perhaps the introduction of domesticated buffalo or diseases associated with livestock are responsible for their demise.

General Methods and Materials

CAPTURE

Tigers were captured for instrumentation using a modified version of an old hunting technique. Basically, capture was accomplished by baiting animals to an area with live domestic buffalo calves placed near dense cover and suitable trees that would provide darting platforms. When the bait had been killed, a funnel-shaped drive was set up (Figure 10), and the tiger was driven off the kill by trained elephants, towards the trees where we waited with dart guns (Figure 11). Range of darting seldom exceeded 20 m.

All individuals (Table 2) were immobilized with the Parke-Davis drug CI-744 (Seidensticker, et al., 1974; King, et al., 1977). The immobilized animal was weighed, measured, tattooed in both ears with an identifying number, and a radio-collar (Figure 12), weighing 0.9 to 1.2 kg, was fastened around its neck (Figure 13). Towards the end of anesthesia (5–7 hrs), all elephants and personnel were removed and the animal was watched from a vantage point 20–100 m away

FIGURE 9.—Villagers cutting grass in park.

TABLE 1.—Large mammals presently found in Chitawan Park (scientific nomenclature of Ellerman and Morrison-Scott, 1951)

Scientific name	*Common name*
PRIMATA	
Macaca mulatta	Rhesus monkey
Presbytis entellus	Common langur
LAGOMORPHA	
Lepus nigricollis	Indian hare
RODENTIA	
Hystrix indica	Indian porcupine
CARNIVORA	
Canis aureus	Jackal
Cuon alpinus	Indian wild dog
Vulpes bengalensis	Indian fox
Melursus ursinus	Sloth bear
Lutra perspicillata	Smooth Indian otter
Prionodon pardicolor	Spotted Linsang
Herpestes edwardsi	Common mongoose
Herpestes urva	Crab-eating mongoose
Paradoxurus hermaphroditus	Tody cat
Viverra zibetha	Large Indian civet
Viverricula indica	Small Indian civet
Arctictis binturong	Binturong
Mellivora carpensis	Ratel
Felis chaus	Jungle cat
Felis viverrina	Fishing cat
Panthera pardus	Leopard
Panthera tigris	Tiger
PROBOSCIDEA	
Elephas maximus	Domesticated Indian elephant
ARTIODACTYLA	
Bos gaurus	Gaur
Sus scrofa	Wild pig
Muntiacus muntjak	Barking deer
Axis axis	Chital, Spotted deer
Axis porcinus	Hog deer
Cervus unicolor	Sambar
PERISSODACTYLA	
Rhinoceros unicornis	Great one-horned rhinoceros

until it was able to walk (Figure 14). One adult tigress died seven hours after darting. A combination of high ambient temperatures, anaesthetic hyperthermia, and her apparent poor condition, contributed to her death. A necropsy showed fractured carpal and metacarpal bones in one forelimb and a gangrenous area in one hip.

Animals were classified as cub, subadult, or adult on the basis of size, weight, dentition, reproductive condition, and birth dates.

In most cases the response of tigers to darting and handling did not indicate that they were disturbed by the process. Some animals returned the same day to feed on the bait kill they were driven off, and in three cases an animal killed a new bait the same day.

RADIO-TRACKING EQUIPMENT

Equipment was supplied by the Bioelectronics Lab of the University of Minnesota, Cedar Creek Natural History Area, Bethel, Minnesota, and operated in 164-165 MHz band.

RADIO-LOCATION PROCEDURES AND METHODS

Aerial photographs of the park were of sufficient quality and scale to provide many reference points such as roads, trails, and other topographic features. The position of a tagged animal was determined by triangulation from known reference points as described by Heezen and Tester (1967). Bearings were taken using a hand compass and locations (fixes) were obtained by plotting the bearings on aerial photographs. Locations were then transcribed onto a map with a 1.8 ha (4.4 acre) grid and these fixes were subsequently assigned coordinate values for computer analysis. This grid size was chosen because most locations were determined from a distance of 0.8 km, and accuracy tests in the field indicated that the average linear error (difference between radio-location and true location) at this distance was ±67 m (N=12).

Animals were located from elephant (65%), vehicle (24%), aircraft (4%), and on foot (7%) using portable receiving equipment (Figure 15). The approximate line-of-sight tracking distances for the different methods in different habitats are shown in Table 3.

Attempts were made to locate each tiger at least once a day, but this was not always possible for most individuals as they ranged over a wider area than we could cover on a daily basis. An

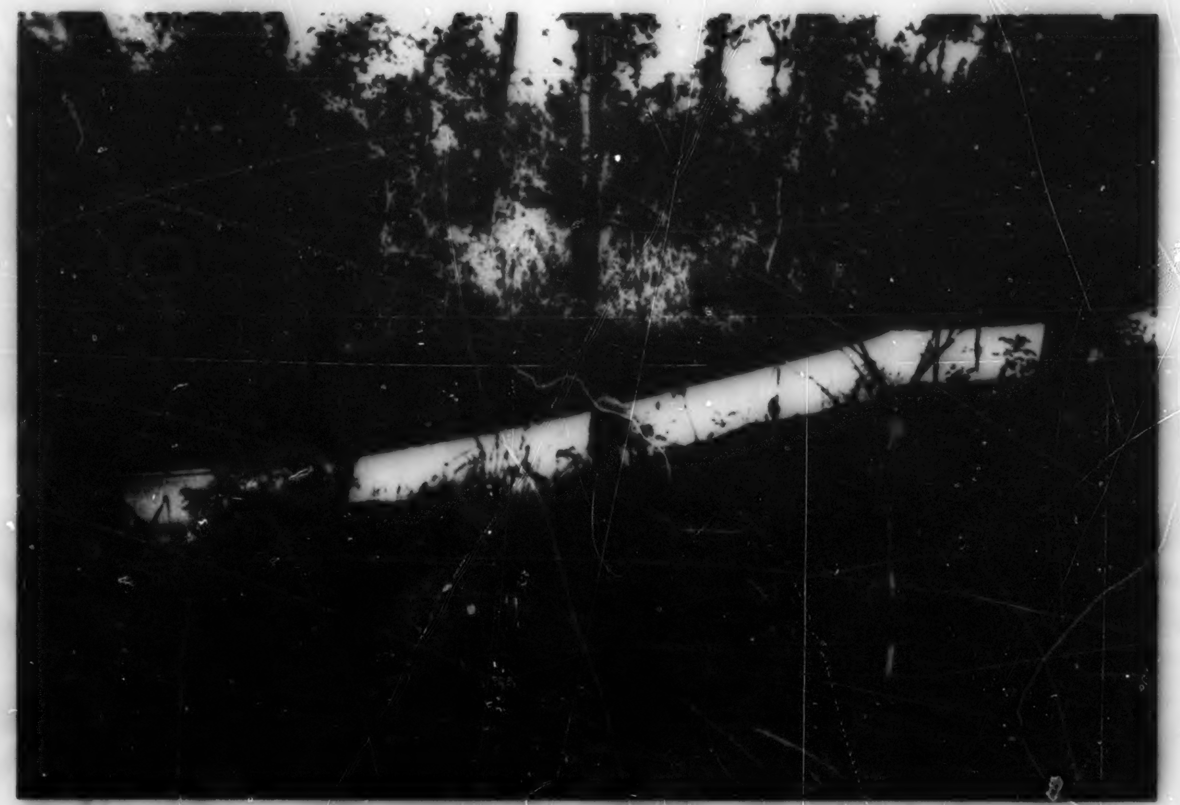

FIGURE 10.—White cloth positioned in undergrowth and forming sides of funnel as part of capture technique.

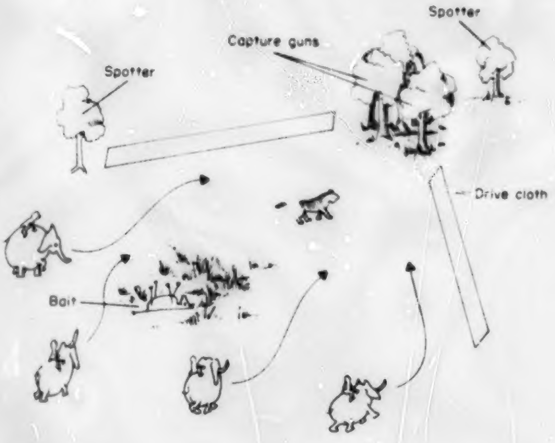

FIGURE 11.—Technique used to capture tigers.

area of about 20 km^2 near camp was searched almost daily, and, as time permitted, other areas were then searched. Our mobility was drastically reduced in the wet season by swollen rivers and impassable roads so location data for this season were correspondingly limited.

A total of seven tigers was radio-tracked for varying periods between December 1974 and September 1976 (Figure 16). The total number of radio-locations for each animal is shown in Table 4.

The effects of radio-collars on the movements and activities of tigers did not appear significant. Tagged animals singly killed large prey, females came into estrus, mated, and successfully reared cubs, and resident animals maintained their

TABLE 2.—Tigers captured in Chitawan Park, 1973–1976 (some animals captured several times)

Tiger no.	*Age/sex*	*Weight (kg)*	*Length (cm)*	*Capture date*	*Remarks*
101[a]	adult F	150	274	18 Dec 73	
101	adult F	164	274	3 Mar 75	
101	adult F	153	274	11 May 76	
102[a]	adult M	200	287	20 Feb 74	
102	adult M	200	292	6 Feb 76	
103[a]	cub F	52	178	21 Mar 74	young of 101
103	subadult F	114	251	23 Jan 75	(litter mate
103	adult F	129	261	26 Dec 75	of 104)
104	subadult M	159	289	17 Dec 74	young of 101
105	adult M	227+[b]	302	31 Dec 74	
105	adult M	227+[b]	310	31 Dec 75	
106	adult F	141	259	16 Feb 75	
106	adult F	141	264	14 May 76	
107	adult F	148	282	15 Feb 76	
108	adult F	116	251	23 Apr 76	died same day

[a] Captured by Seidensticker and Tamang.

[b] Scale only weighed to 227 kg (500 lb).

home ranges. Whether our presence in the area was disturbing is difficult to evaluate, but since most locations were determined from a distance of 400 m or more the animals were probably not even aware of us.

Population Characteristics

NUMBERS AND COMPOSITION

At the beginning of 1976 there were at least two, probably three, resident males in the park. One male (105) ranged over the northeast portion and another (102) ranged over the western sector and onto the islands in the Narayani River. Neither 102 nor 105 was located in the southeast part of the park, indicating there was space available for another resident. Tracks of an adult male were found in this area on several occasions, and it seems likely that a third male was resident there. Since this study was terminated the park has been expanded to almost twice its original size and the number of resident males is currently estimated at six (J.L.D. Smith, 1978).

In early 1976 the number of resident tigresses in the park was estimated at 12, of which eight were individually identified. Three tagged females (101, 103, 106) resided in the northeast and another adult female was captured in the area in early 1976, but since she died the same day her status is unknown. Five females resided in the western half of the park; one of these (107) was radio-collared, and the others were identified by McDougal (1977). An additional two or three

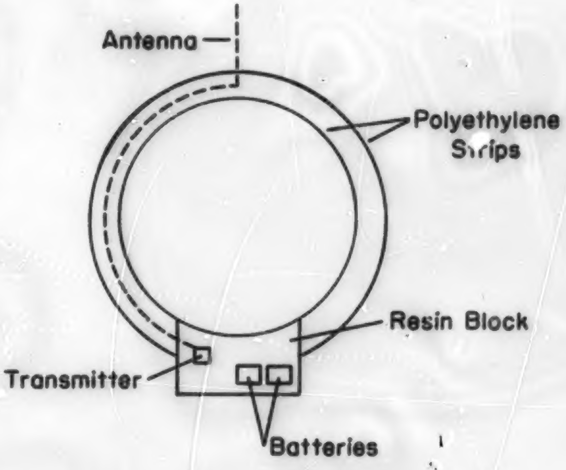

FIGURE 12.—Diagram of radio-collar.

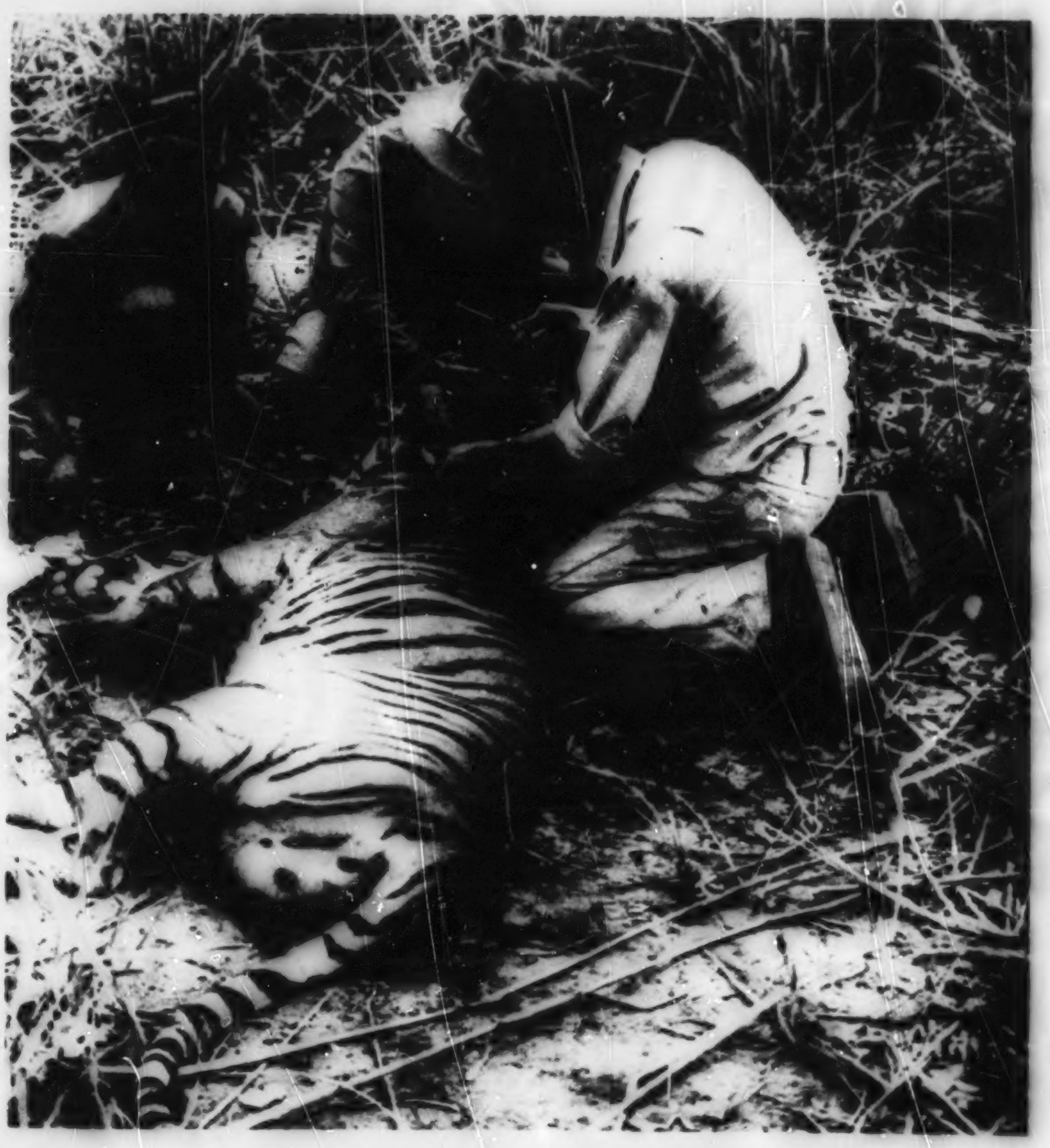

FIGURE 13.—Attaching radio-collar to immobilized tigress.

females (based on tracks) resided in an area south of the Churia Hills, and on the islands in the Narayani River there were probably one or two more females (McDougal, 1977). The number of resident females is a minimum estimate since additional females may have resided in the upland sal forest areas of the Churia and Someswar Hills. In the expanded park J.L.D. Smith (1978)

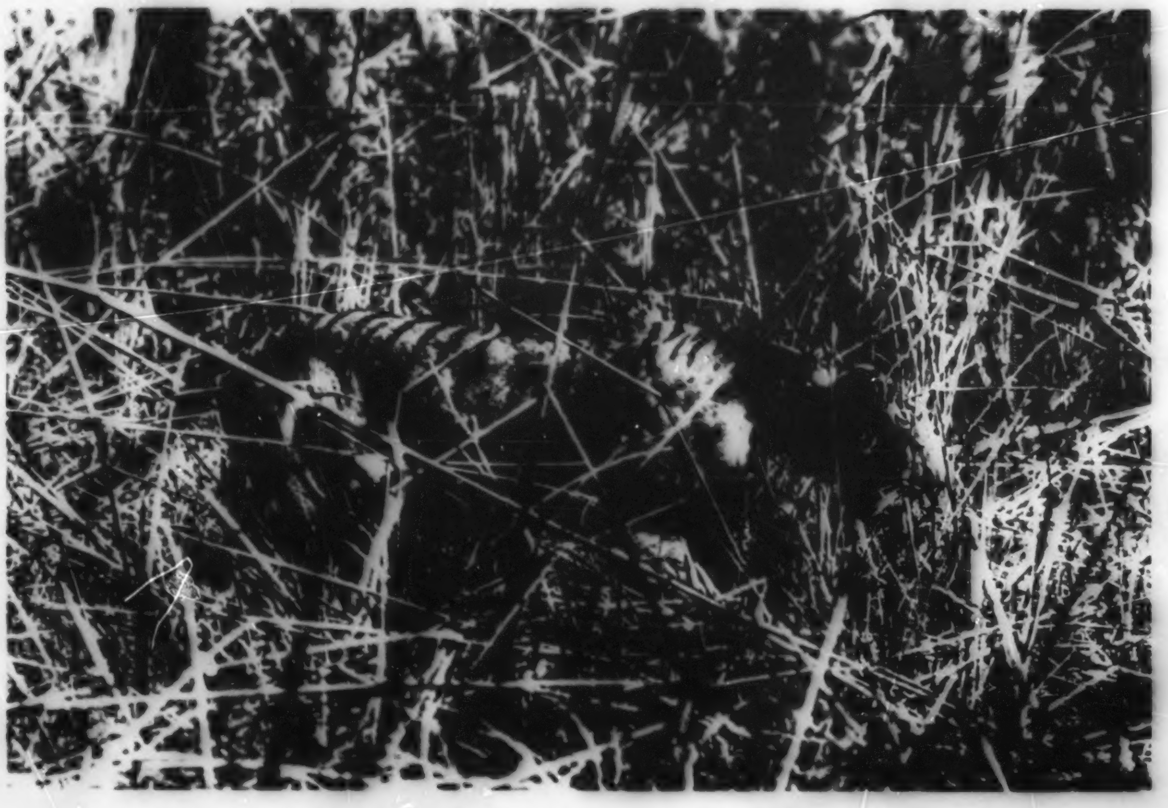

FIGURE 14.—Collared tigress walks off after recovery from anesthesia.

estimates there are 18 resident females.

The disproportionate sex ratio of adults, 1 : 3-4 favoring females does not appear to be unusual. Several workers have made similar observations (Rice, 1857; Sanderson, 1896; Hicks, 1910; Lydekker, 1924; Locke, 1954; Schaller, 1967; Sankhala, 1977).

In addition to an estimated 15 resident adults, there were at least 14 pre-dispersal offspring in the park in early 1976. These included two subadult males, two subadult females, six large cubs and four small cubs. Additional young were probably present in the areas that were infrequently searched. In total, the number of tigers in the park in early 1976 was estimated at 32. The number of tigers whose ranges are not wholly included in the park or who moved through as transients is not known, but only three different transients were observed in the northeast section during the study.

The number of resident animals appears to be fairly stable. McDougal (1977, pers. comm.) observed that over a 7-year period (1973-1979) the number of residents at the western end of the park changed from three to four. Similarly, between 1975 and 1979 the number of residents in the northeast has gone from four to five (J.L.D. Smith, 1978, pers. comm.; this study). Some individuals have resided in their respective areas for several years (see "Home Range"), and while there have been changes in occupancy and shifts in ranges, there appear to be only so many slots available under present environmental conditions.

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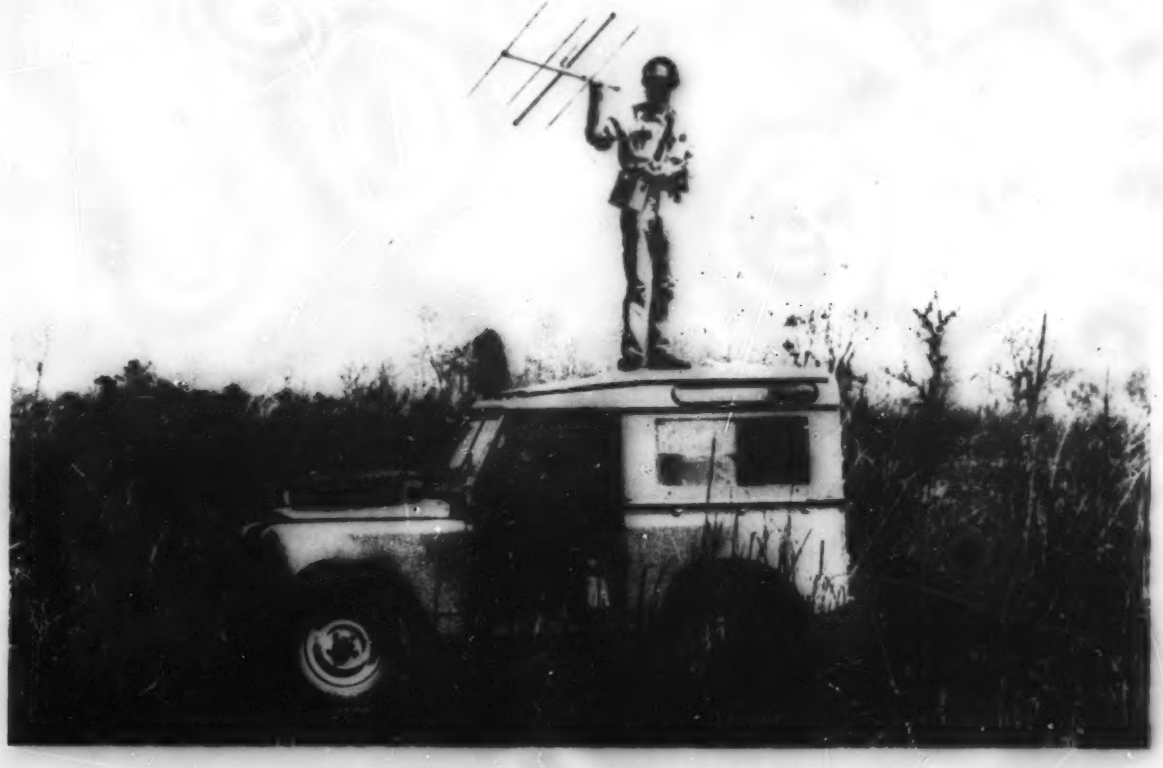


Figure 15.—Directional antenna attached to receiver used to electronically search an area for signals from radio-collared animals.

Table 3.—Approximate range of reception (km) for radio-tracking tigers with different methods in different habitats

Method	*Grassland*	*Riverine*	*Sal forest*
Elephant	3.2	2.4	0.8
Vehicle	3.2	2.4	0.8
Air*	16.0	16.0	13.0
Foot	1.6	1.0	0.4

* Aerial tracking distances from altitude of 350–450 m.

Density

The estimated crude density of adult tigers within the original park (544 km^2) boundaries is one per 36 km^2; in the expanded area (932 km^2) it is one per 39 km^2 (J.L.D. Smith, 1978). Areas of prime habitat, however, or those containing an interspersion of riverine forest and grassland support higher tiger densities. For example, a 62 km^2 area in the northeast had four residents or one per 15.5 km^2; another area (91 km^2) at the western end had one adult per 22.7 km^2 (McDougal, 1977). A recent survey by J.L.D. Smith (1978) showed that in a 245 km^2 area of prime habitat there were at least 18 tigers over two years of age, or one animal per 13.6 km^2. Preliminary surveys in areas (i.e., sal forest) lacking the interspersion of habitats indicates they support only about one-third the density recorded in prime habitats (J.L.D. Smith, 1978).

Table 5 compares estimates of tiger densities from a variety of studies in different habitats. The

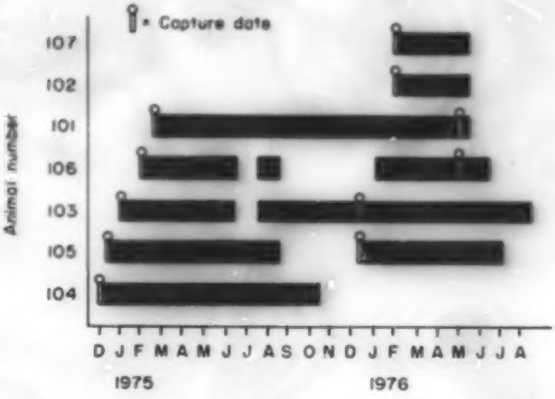


FIGURE 16.—Times when individual tigers were monitored by radio-tracking.

TABLE 4.—Radio-location data of tagged tigers

Tiger no.	*Age/Sex*	*No. of locations*	*No. of days located*
101	adult F	391	246
102	adult M	16	12
103	subadult F	198	125
103	adult F	245	157
104	subadult M	218	155
105	adult M	203	138
106	adult F	135	115
107	adult F	16	14
Total		1422	962

habitat suitability in Chitawan appears to be good to excellent, based on this comparison of tiger densities in other locales. Tropical rainforest ranks low, as do the mixed coniferous/deciduous forests in the Soviet Far East.

REPRODUCTION

Tiger reproduction in Chitawan is high, as at any given time during this study most resident tigresses either had young or they were pregnant. Of the eight resident females individually identified in 1976, no fewer than six had a total of 14 young. J.L.D. Smith (1978) reports that of eight resident females in April 1978, seven had a combined total of 20 young and the other was probably pregnant. High productivity in Chitawan accounts for a surplus; more animals are reaching maturity than there are available vacancies (resident mortality), and the rapid filling of vacancies suggests that reproduction will be sustained at the current high rate. In comparison, a biennial survey (1972–1978) in Kanha Park, India, showed an average of 38% (range 25%–43%) of resident females to have young (Panwar, 1979).

AGE OF SEXUAL MATURITY

Data from zoos indicate that tigers usually reach sexual maturity or produce their first litter when three to six years old (Sankhala, 1967; Schaller, 1967). Little data are available from the wild. McDougal (1977) reported a male reached sexual maturity when three and one-half years old. In this study, a subadult male (104) estimated to be 30 months old was judged to be sexually immature, whereas his sister (103) at this same age showed behavior indicating the onset of estrus, although she did not produce a litter until about 40 months old.

ESTROUS CYCLE

Most of the zoo data indicate that tigresses have a 50-day estrous cycle and mean heat period of seven days (Sadleir, 1966; Kleiman, 1974), although Sankhala (1967) reported that estrus occurred every 15–20 days between December and May, and Crandall (1964:385) notes heat recurring at about 3-week intervals. The limited data from this study support those of Crandall (1964), but it should be noted that most of the observations were on one female (103) who was coming into heat for the first time. For tigress 103, the interval between bouts of roaring (Schaller, 1967:258) and/or visits by an adult male, which were used as indicators of a heat period, was monitored from mid-October 1975 to mid-April 1976. She was heard to roar and was visited by an adult male during the first five suspected heat periods, after which heat periods were indicated only by the male's presence (Table

TABLE 5.—Estimates of tiger densities from a variety of studies in different habitats

Location	*Total area (km²)*	*Estimated No. resident adults*	*Crude density (N/100 km²)*	*Crude wild ungulate biomass (kg/km²)*	*General vegetation characteristics*
Chitawan[1]					
Original	544	15–20	2.8–3.7	1673–2589	Moist, semi-deciduous forest/ gallery forest and alluvial plain
Expanded	932	21–24	2.3–2.6	-	Same as above
Kanha Park[2]					
Original	319	10–15	3.1–4.7	663	Moist, semi-deciduous forest with meadows
Expanded	940	30–40	3.2–4.3	1250	Same as above
Sundarbans, West Bengal[3]	5960	280	4.7	1250	Moist, tropical, beach and tidal forest
Ujung Kulon, Java[4]	300	3–4	0.75–1.0	492	Tropical evergreen forest with meadows
Sihote-Alin Reserve, USSR[5]	3100	6–7	0.2	-	Mixed coniferous and deciduous forest
Lazovski Reserve, USSR[5]	1160	7–10	0.6–0.9	-	Same as above

[1] Chitawan data from McDougal (1977), J.L.D. Smith (1978), Tamang (1979), Seidensticker (19/6b), and this study.

[2] Kanha data from Schaller (1967), Panwar (1979), Coe (1979).

[3] Sundarbans data from Hendrichs (1975).

[4] Ujung Kulon data from Hoogerwerf (1970), as cited in Seidensticker, et al. (1980).

[5] USSR data from Matjushkin, et al. (1977).

17). These data indicated the interval between the mid-points of five consecutive estrous periods was 25 days (range, 20–30 days). On the projected date for the sixth estrous period 103 was not heard to roar and male 105 was not located with her, although he was in her area at that time. They were, however, located together in mid-March and again in April; the interval between these visits was 24 days. Female 103 did not, however, have young until late October 1976, which means conception occurred in mid-July. For a sexually experienced female (101), using only the male's association with her as an indicator of a heat period, the interval between the mid-points of two consecutive estrous periods was 24 days.

J.L.D. Smith's (1978) observations on the timing of associations between a young adult female and an adult male suggest an even shorter estrous cycle. He found the two animals together at regular intervals from December to April, with the associations invariably falling on the fifth or sixth and 20th or 21st of each month. These data tend to support the 15–20 day cycle reported by Sankhala (1967).

The apparent disparity in cycle length suggests a certain amount of variability exists between individuals, possibly depending on sexual experience, pseudo-pregnancy (Asdell, 1964), or that periodic associations are occurring at times other than true heats. Lions (Schaller, 1972; Eaton, 1978) and captive tigers (Kleiman, 1974) copulate and show estrous behavior when not in heat. Sexual activity did, however, seem to be involved in the associations recorded in this study, as evidenced by the dramatic shift in interest displayed by the resident male (105) toward female 103 before and after her first suspected heat (see "Social Interactions"); and that this same male, while not being found with female 101 in the month before her young were born, was located with her on several different occasions shortly after her newborn young died.

The average length of the heat period, based on the number of consecutive days female 103 was heard to roar, was five days (range, two to seven days, N=5). Male 105 was, however, never located with either 103 or 101 for more than two consecutive days, suggesting that their heat periods were short or that his visits did not coincide with peaks of receptivity. It is also possible that no mating occurred between female 103 and male 105 because she was intimidated by the proximity of a large male with which she was not used to associating. A successful mating did occur, eventually, and 103 and 105 have subsequently mated successfully on two other occasions (J.L.D. Smith, pers. comm.), although the longest association he has recorded between any pair is two days. Some of these have resulted in conception.

Seasonality of Mating

Tigers in India may mate and give birth at any time of the year (Sankhala, 1967; McDougal, 1977), but the cool and early part of the hot season (November to April) appears to be the peak time for sexual activity. Vocalizations are most frequent from November through February (Perry, 1964; Schaller, 1967; McDougal, 1977; this study), and it is during this time that most adult male-adult female associations are recorded. McDougal (1977), for example, found a male and female together every month between November and May; another female associated with a male on at least one occasion during every month from October to April. I recorded a similar pattern, with associations between one pair occurring almost monthly between October and April; and J.L.D. Smith (1978) found a male and female together at regular intervals from December to April. Repeated associations over such a long period suggest that the conception rate is low, assuming of course that mating occurred. The conception rate of tigers in zoos is low, about 29% (Kleiman, 1974). Conception rates of lions in the wild are also low, about 40% (Schaller, 1972; Eaton, 1978). In the wild it appears that tigers unsuccessfully bred early in the season are continuing to cycle, but for how long and at what intervals is not known. In zoos, fewer estrous cycles occur from April to September (Kleiman, 1974).

Backdating from birth dates using a gestation period of 104 days (Kleiman, 1974; Sankhala, 1977), six litters in this study were conceived in December–January (3), July (1), and September (2). Similarly, McDougal (1977) estimated that for 12 litters, eight were conceived between October and April, and four in July–August. This sample is not large enough to indicate a peak time for births, but it does show, along with the observations on vocalizations and the timing of associations, that sexual activity is high in the cool season and early part of the hot season.

Litter Size and Sex Ratio

Litter size in the wild varies from one to seven (Brander, 1923), but tigresses are seldom seen with more than three young. This is not an accurate measure of litter size at birth and there is little information on pre-natal litters. In zoos, the average litter size at birth is about 2.8 and the sex ratio is parity (Schaller, 1967; Sankhala, 1967).

Reproductive Potential

Tigers have a high reproductive potential. In zoos, when the cubs are removed from the mother at birth, one litter per year is common (Schaller, 1967). In the wild, if the young survive, a tigress produces a litter about every two to two and a half years. Estrus is apparently suspended until the young are independent, although there are reports of pregnant tigresses being shot while accompanied by young less than a year old (Stewart, 1927; Hewett, 1938). In two cases reported by McDougal (1977), one female was estimated to have had young in August (1972) and the next litter in March (1975), an interval of 31 months;

another had young in December (1972) and again in May (1975), an interval of 29 months. A tigress in Kanha Park had young in January–February (1969) and 30 months later (June–July 1971) she again had young; her next litter was born in July (1973), 25 months later (Panwar, 1979). In this study a tigress (101) who was estimated to have had young in April–May (1973), had her next litter in early April (1975). This litter was lost in a grass fire shortly after birth, and she apparently came into heat 17 days later (see "Social Interactions"). Sadleir (1966) reports that in seven instances, from 16 to 56 days (mean 28) elapsed between removal of young and return of estrus. In three instances recorded by Sankhala (1977), the interval was 10, 12, and 29 days. Thus a tigress is potentially able to produce a new litter within four to five months of having lost one. The tigress that lost her young in mid-April 1975 did not, however, have a new litter until mid-December 1975, eight months later. Thus, she did not conceive until four and one-half months after loss of the litter. This third litter was lost in late February 1976, and 10 months later she produced a fourth litter; thus conception occurred about six and one-half months after her young died. Overall, tigress 101 bore four litters in a period of 44 months.

The total lifetime production of a tigress living under optimum conditions in the wild is probably 13 to 18 animals, but only about half that number are likely to reach adulthood. This assumes she reaches sexual maturity at about four years old, and produces a litter of three every two to two and one-half years until she is 15 years old. The age at which tigresses in the wild cease to reproduce is not known, nor is the life expectancy known, but in zoos sexual activity and births are reported in 14-year-old females (Crandall, 1964: 388; Kleiman, 1974).

MORTALITY

Causes of mortality among young and subadult tigers are numerous (see Schaller, 1967:233), and while adults have few mammalian enemies, more probably die as a result of hunting, trapping, poaching, and poisoning than from any other cause (Schaller, 1967).

In this study, three (11-day-old) young from one litter perished in a grass fire; another litter, when two to three months old, was lost to unknown causes. A male estimated to be 16–17 months old (based on earlier photographs, McDougal, 1977), who should have weighed about 140 kg, voluntarily entered the kitchen of a guard station on 5 July 1975. He was in an emaciated state, weighing only 49 kg, and he died the following day. Necropsy revealed a porcupine quill embedded in one shoulder. There were no signs of external injury; it was surmised that the quill had disabled the tiger to the extent it was unable to hunt and this led to its death. One adult female died of unknown causes in 1975; her carcass was found by guards near the park's edge. Male 102 and female 106 died in 1976, and poisoning was strongly suspected as the cause of death. The male was about six years old at the time of death (McDougal, 1977); 102's remains were found at the park's edge and the female's were found near a domestic buffalo carcass just outside the park (Smith and Tamang, 1977). Villagers near the remains had complained of tigers taking domestic livestock. When livestock are killed, tigers may be killed by poachers or local villagers who place pesticides or other poisons in livestock carcasses.

MORTALITY RATE

No precise estimate of mortality rate of young tigers can be determined since the litter size at birth is unknown and the fate of young is often unknown. There are, however, a few reports that indicate the extent of mortality among the young. In Kanha Park, one tigress raised four young to at least 16 months old while another tigress lost three of four young before they were three months old, or 38% mortality in the first year (Schaller, 1967). Singh (1973) reported that three of seven young, from three litters, perished before they were two years old, a mortality of 43% for the first two years of life. In Chitawan, McDougal (1977) reported that of 14 cubs (six litters) belonging to four different tigresses, two young probably died in the first year and two probably died in their second year of life, or about 31% mortality in the first two years of life. In this study, of four litters born to one tigress, two young from the first litter survived to at least three years old. Three young from the second litter died, no young from the third litter survived, and three young from the fourth litter survived to at least one year of age (J.L.D. Smith, 1978). If the litter size of the first and third litter is assumed to be two, then the mortality rate for the first year is about 50%. Although the data on cub mortality are limited, it is probably not unreasonable to assume, as have Schaller (1967), Singh (1973), and McDougal (1977), that the mortality rate during the first two years of life is at least 50%. By comparison for two lion prides in the Serengeti, Schaller (1972) estimated a minimum mortality rate of 67% during the first year of life.

Activity Patterns

Methods.—Audible qualities of radio signals were used to interpret activity (Lord, et al., 1962). An animal was considered active if its signal changed in tone or strength during the three to five minutes required to obtain a bearing. It was not possible to classify the type of activity, and movement was determined only from changes in an animals's location. Most bearings were determined from a distance of about 0.8 km, and thus activity interpretation was not biased by the investigator's presence. There is a bias toward activity because slight movements by a tagged individual can cause a change in signal tone.

Data were pooled for all available animals (N=7); thus individual differences in activity are masked. Each bearing was scored active or inactive, summarized by 1-hour intervals, and the percent active in each interval was computed. Data were then summarized by season. In the statistical analysis of activity patterns, nocturnal data were excluded because sample sizes were too small for most seasonal comparisons. Data were excluded if an animal was disturbed by our radiotracking activities.

Results.—Tigers were active and moving primarily at night, although some daytime activity and movement was not uncommon. The seasonal activity patterns are shown in Figure 17. Data for males and females were pooled because they

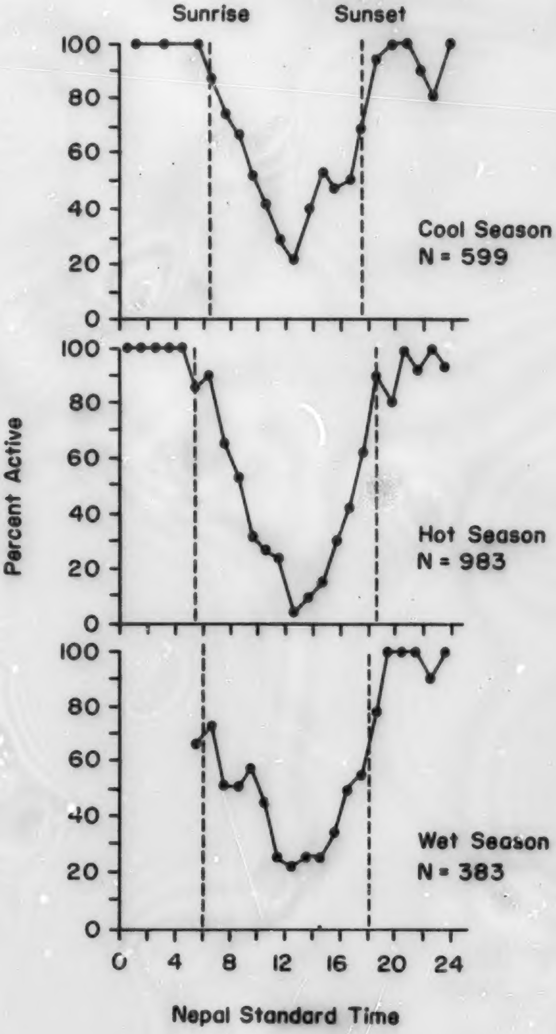


Figure 17.—Seasonal activity patterns of tigers in Chitawan Park (N = number of activity records).

showed no significant seasonal difference in the amount of daytime activity (Table 6).

Tigers were least active from mid-morning to mid-afternoon in the cool season (October–February). Levels of activity decreased gradually during the morning, and at the low point (1100–1300 hrs), about 75% of the animals were inactive. Activity increased beginning in mid-afternoon, peaked shortly after sunset, and remained high until midnight. All of the few records obtained between 2400 and 0500 hrs indicated activity.

Daytime activity during the hot season (March–May) was markedly reduced, particularly from mid-morning to mid-afternoon. Activity decreased gradually after sunrise and by mid-morning about 75% of the records indicated inactivity; by noon it was 95%. Activity increased slightly from 1300–1500 hrs and then rose sharply in the hour before sunset, by which time 90% of the records indicated activity and the level remained high throughout the night.

Levels of daytime activity for the wet season (June–September) were somewhat irregular, but tigers were generally inactive from mid-morning to mid-afternoon and then activity increased. By sunset most tigers were active, and remained so at least until midnight, after which no data were collected.

TABLE 6.—Seasonal comparisons of daytime activity of tigers in Chitawan Park

Seasons/time of day	*Chi-square value*
Females > males (0600–1800 hrs)	
Cool	0.868
Wet	2.436
Hot	4.391
Males and females combined (0600–1800 hrs)	
Hot > wet	0.886
Cool > hot	1.666
Cool > wet	3.326
Males and females combined (0900–1600 hrs)	
Cool > wet	0.069
Wet > hot	7.347[a]
Cool > hot	14.119[b]

[a] Significant at 0.05α, 2df.

[b] Significant at 0.01α, 2df.

As shown in Figure 17, tigers are likely to be active 15–16 hours/day, but cessation or onset of activity is not associated with sunrise or sunset. They are, however, essentially nocturnal, as shown by the proportion of records classified as active during daytime and night (Table 7). Similarly, leopards residing in the same area are primarily nocturnal, but they show significantly less activity than tigers during daytime (X^2=78.34, P<.01) and at night (X^2=25.8, P<.01). By comparison, leopards in Tsavo Park, Kenya, are also essentially nocturnal (Hamilton, 1976).

There was no significant difference in the amount of daytime activity between seasons except when comparisons were limited to only the hottest part of the day (0900–1600 hrs). Under these conditions there was significantly less activity during the hot season than in the other two (Table 6). While average maximum temperatures in the hot season are only slightly higher than in the wet season, 36°C vs 33°C, tigers were significantly less active.

Tigers were occasionally found moving during the hottest part of the day (all seasons), but they were less likely to do so in the hot season. Animals located about mid-morning in the hot season were relocated one to six hours ($\bar{X}$=2.5 hr) later in the same place about 82% of the time (N=73).

TABLE 7.—Comparison of the activity of Chitawan tigers and leopards with the activity of leopards in Tsavo Park, Kenya (Tsavo data from Hamilton, 1976)

Period	*Chitawan*		*Tsavo*
	Tigers (N = 7)	*Leopards (N = 5)*	*Leopards (N = 10)*
Daylight	(0600–1800 hrs)		(0600–1900 hr)
Total activity records	1431	245	1189
Percentage active	42%	12%	20%
Dusk to sunrise			
Total activity records	534	91	154
Percentage active	92%	74%	71%

By comparison, animals located about mid-morning in the cool season were relocated one to six hours ($\bar{X}$=3.0 hr) later in the same place about 64% of the time (N=48).

DISCUSSION.—Tigers in Chitawan are usually active and moving between sunset and sunrise, but the light-dark cycle does not appear to control their activity patterns since some daytime activity and movement is common and activity periods are not marked by an abrupt cessation or onset associated with sunrise and sunset. In the older literature reviewed by Perry (1964), tigers are reported to be primarily nocturnal or crepuscular, but these reports are based on circumstances when tigers were heavily hunted, and their activity patterns may have been affected by hunting, as reported for lions (Rainsford, 1909). For a sanctuary population, Schaller (1967) reported greatest activity at night with resting between mid-morning and mid-afternoon, although an animal sometimes hunted throughout the day after an apparently unsuccessful night.

Daytime activity is, however, significantly less in the hot season, suggesting the influence of temperature on activity. In the hot season tigers in Chitawan frequently rested in dense cover along permanent streams (see "Habitat Use") and they were probably lying in the water, as observed by Schaller (1967), Singh (1973), and others in India. Similarly, leopards are usually inactive during the hottest part of the day and do not frequently spend the day in the open exposed to the sun (Eisenberg and Lockhart, 1972; Schaller, 1972; Hamilton, 1976). Lions, on the other hand, do not seem to be affected by high ambient temperatures (Schaller, 1972:123).

These congeneric differences in response to high ambient temperatures support Kleiman and Eisenberg's (1973:638) observation that the "evolutionary sequence in *Panthera* has been an initial adaptation away from moist, warm biotopes and a gradual successive invasion of cool, moist biotopes by the tiger and dry tropical areas by the leopard. An ultimate adaptation of the lion occurred to dry, open savanna conditions."

High daytime temperatures do not, however, appear to reduce the activity of females with young. Seidensticker (1976a) radio-tracked a tigress in Chitawan from mid-December 1973 to mid-April 1974 and found her active in 91% of location records between 0500–1000 hrs, 80% between 1000–1600 hrs, and 83% between 1600–2100 hrs. This animal showed almost twice as much daytime activity as recorded in this study (Table 7), and in March–April 25% of the location records between 1000–1600 hrs indicated movement. She did, however, have two 6–10-month-old young, and she may have had to extend her hunting efforts into the daytime to secure food for herself and her young. The rate of killing by this tigress was higher than for females in Chitawan without young (see "Kill Rate"), suggesting that females with young may not be more efficient but make more kills by increasing their hunting time. Having small young localizes the movements of the female, thus probably making it more difficult for her to regularly secure prey from the same relatively small area as ungulates may leave the vincinity. This has been observed by Sinha (1979a); and by Hornocker (1970) with respect to mountain lions. That females may have difficulty procuring food for their offspring is also suggested from baiting records. McDougal (1979) recorded significantly greater use of bait sites by females with large but dependent young than for females with small young or those without young.

A major portion of a predator's time and energy are expended in locating and securing food; this is reflected in the close similarity between the activity patterns of the tiger and its prey. The basic activity patterns of chital, hog deer (*Axis porcinus*), and sambar (*Cervus unicolor*) are as follows.

Chital have two peaks of feeding, one between 1700–1900 hrs, followed by a rest between midnight and early morning, and another between 0500–0700 hrs, with a rest again from mid-morning to mid-afternoon (Schaller, 1967; Seidensticker, 1976b; Dinerstein, 1980). All three authors note that daytime activity of chital appears related to the intensity of solar radiation. In the cool season chital are active for longer periods in open grasslands and savannas on cloudy days and cool mornings, whereas in the hot season they are seldom seen in open areas from mid-morning to late afternoon. On cloudy or rainy days in the monsoon season chital are occasionally seen to graze in the open, even at midday.

The activity pattern of hog deer is similar to that of chital except there may be an additional peak of feeding activity about 1000–1100 hrs, and hog deer usually appear earlier and stay longer in open areas (Seidensticker, 1976b). The nocturnal activity pattern of hog deer is not known.

Sambar are primarily nocturnal, being found in open areas at night, but they retreat into the forest by dawn and do not emerge again until late afternoon or early evening (Schaller, 1967; Seidensticker, 1976b; Dinerstein, 1980).

Because prey are likely to be active at somewhat different times, a variable activity pattern may be necessary for tigers for which vision and hearing play important roles in hunting. When prey are active they are presumably easier to find and to stalk. Indeed, the structure of the domestic cat's retina is such that a motionless, cryptic prey might not be detected (Fox, 1974). It is not known if tigers are more successful catching prey during certain periods of the day, but fresh kills of several prey species were found in late afternoon, at night, and early to mid-morning.

Observations on other large cats also indicate that they may vary their activity schedules to correspond with changes in activity of prey. Seidensticker, et al. (1973) observed that mountain lions increased their daytime activity in summer, apparently in response to diurnal activity of Columbian ground squirrels (*Spermophilus columbianus*), a prey not available at other times of the year. Asiatic lions (*P. leo persica*) in the Gir Forest, India, have shifted from feeding on wild prey to preying on domestic animals. In the process, their activity also changed from nocturnal to being diurnal (Joslin, 1973). Lions in the Serengeti are more variable, being nocturnally active in areas lacking cover and often hunting during the daytime in areas with cover, especially when prey are concentrated (Schaller, 1972). Lions in Nairobi and Ngorongoro differ in that they are basically nocturnal (Rudnai, 1973; Estes, 1967), a pattern that may be in response to tourist activities (H. Rood, pers. comm.). The sporadic occurrence of diurnally active prey in the diet of leopards also indicates that they are not strictly nocturnal (Eisenberg and Lockhart, 1972; Schaller, 1972; Hamilton, 1976).

Leopards in Chitawan are primarily nocturnal but their activity patterns may be influenced by the presence of tigers. While leopards in Tsavo Park, Kenya, are essentially nocturnal, lions are also present there (Hamilton, 1976). In Sri Lanka and in several African parks, where only leopards occur, they are reportedly less nocturnal and more terrestrial than in areas where they coexist with either tigers or lions (Eisenberg and Lockhart, 1972; Muckenhirn and Eisenberg, 1973; Myers, 1976). Chitawan leopards are significantly less active than tigers during daytime and at night, which may reduce the possibility of unexpected encounters, or they may be employing a slightly different hunting strategy (more pauses to look and listen), which again could be related to the presence of tigers. Leopards in Chitawan also use roads much less frequently than tigers (see "Movements"), thereby probably reducing confrontations with the socially dominant tiger (Morse, 1974). On one occasion a bait killed by a tagged leopard was, after an audible scuffle, appropriated by a tagged tiger. Overt interactions, including leopards being killed by tigers at bait stations, are known from Chitawan (McDougal, 1977). Seidensticker (1976a) radio-tracked a resident tigress and a resident female leopard in Chitawan, and while their ranges overlapped extensively, the two cats differed in activity periods, habitat use, and size of prey killed (see "Prey Size"). He concluded that coexistence in Chitawan is facilitated by a large prey biomass, an abundance of small-sized prey, and dense vegetation structure. An essentially closed habitat may well explain why leopards in Chitawan appear to be primarily terrestrial. Uncollared leopards were observed in trees on only three occasions in two years, tagged leopards were never located (336 locations) in trees, and only one kill was found in a tree.

The seasonal activity patterns of tigers appear to be influenced by several environmental factors, including the activity schedules of prey, possibly temperature, and while there was no significant difference in the amount of daytime activity between the sexes, there may well be fine-grained intra-specific differences depending on social status or reproductive condition. Alternatively, individuals may be active (moving) at the same time of day, but utilize space preferentially or differentially, as suggested from data on habitat use.

Habitat Use

Methods.—The frequency with which tigers used different habitat types in the northeast section (60 km^2) of the park was determined primarily from radio-locations. Data were pooled by sex (three female, two male), thus masking individual differences in habitat availability and use; although each female's range contained a similar extent of riverine forest and grassland, and the two males travelled over the same area. Locations were referenced to a specific grid square, each 1.8 ha (4.4 acres) in area. Three habitat classifications were used: sal forest, grassland, and riverine forest. If a location fell in a grid square containing more than one major habitat type, the location was assigned to the dominant (canopy) type. This convention obscured use of ecotone, more so for grassland/riverine forest than for other mixed vegetative types. Analysis was restricted to seasonal differences in use because sample sizes for some months were too small. Location data were excluded for tigresses with small (non-following) young.

The percentage of locations falling in the sal forest was adjusted because on days when an animal was not found in the grassland and riverine forest areas of its home range, it almost certainly was in the sal forest. The range of signal reception in this habitat was short (Table 3), and only about half of the sal forest in the northeast could be effectively searched, even by vehicle. Of the 165 locations presumed to have been in sal forest, 111 were for females and 54 were for males. Of these 111 locations, 34, 57, and 20 were for the cool, hot, and wet seasons, respectively. These presumed locations represent 14%, 11%, and 11% of the seasonally adjusted data for females. Of the 54 male locations, 17, 31, and six were for the cool, hot, and wet seasons, respectively. These presumed locations represent 16%, 14%, and 12% of the seasonally adjusted data for males. The total number of locations, actual and presumed, was 1468.

Seasonal differences in three habitat components were roughly evaluated in relation to habitat use by tigers. The importance of water was measured as the proximity of locations to permanent water sources. Cover density or habitat complexity was qualitatively assessed as: open, marginal, or dense. The distribution and availability of prey was inferred from habitat affinities, density estimates, and observation.

Results.—Tigers preferred riverine forest and grasslands (Table 8), using these habitats out of proportion to their availability, and sal forest was

Table 8.—Habitat use of tigers in Chitawan Park (N = number of locations)

Habitat/Season	*Riverine forest*	*Grass-land*	*Sal forest*
Approximate % of habitat type available	10	20	70
Percent of total locations (N=1468) in each type for both males and females	28	52	20
Percent of locations (N=1037) in each type by season for females			
Cool (N=238)	49	38	13
Hot (N=599)	20	54	26
Wet (N=200)	53	29	18
Percent of locations (N=431) in each type by season for males			
Cool (N=124)	27	56	17
Hot (N=252)	8	79	13
Wet (N=55)	15	54	31

used much less than expected (X^2=1,115.5, 4df, p<.001). Overall, females used riverine forest much more often than males, who used grasslands more than did females; both sexes used sal forest about equally. On a seasonal basis, however, there were significant differences in habitat use between and within the sexes (Table 8). Males and females differed significantly in their seasonal use of sal forest (X^2=14.387, 2df, p<.01) and riverine forest (X^2=10.791, 2df, p<.01), although not in their use of grasslands (X^2=2.135, 2df, P>.05). Females showed no significant difference in habitat use between the cool and wet seasons (X^2=4.51, 2df, p>.05), but use in the hot season differed significantly from the other two. This difference is related to changes in the frequency of use of all habitat types. Males showed a similar pattern, with differences in habitat use between the cool and wet seasons being insignificant (X^2=5.825, 2df, P>.05), while use in the hot season differed significantly from the other two. This difference is related to changes in the use of riverine forest and grasslands.

In the cool season females were found in riverine forest more often than in grasslands, while males were located in grasslands about twice as often as in riverine forest (Figure 18). Both sexes were infrequently located in sal forest, although use of this type increased as cover was reduced in the grasslands by cutting and burning, and ungulates moved to unburned forest areas. Riverine forest is not burned until after the grasslands, and sal forest is burned last, beginning early in the hot season. Prior to these activities cover in grasslands and riverine forest was dense, whereas it was marginal in sal forest. Water sources are readily available in the cool season, but only 18% of female locations (N=204) and 27% of males' (N=107) were within 0.4 km of water.

In the early part of the hot season, as a result of further burning, cover is marginal in grassland/riverine forest areas and sal forest is open. However, the effect on the grassland is temporary. Grass shoots appear within two weeks after the fires, and they attract many herbivores who feed on the new growth; a month later the new growth is about 80–90 cm high. Tigers utilized grasslands more during the hot season than at other times, probably in response to prey concentrations, but water and/or cover along watercourses may also be important. Almost 45% of the hot season locations for females (N=542) and 72% of those for males (N=221) were within 0.4 km of water, and most of these were in tall grass areas bordering permanent streams.

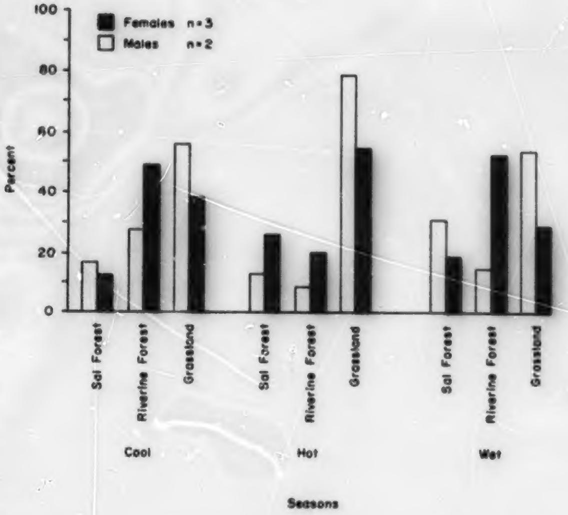


FIGURE 18.—Seasonal use of habitat types by male and female tigers in Chitawan Park.

Cover in sal forest is marginal in the wet season, but in the other habitats it is dense. Water is readily available, and only 21% of the locations of females (N=180) and 44% of those for males (N=49) were within 0.4 km of water. During this period females were located most frequently in riverine forest, and males were found most often in grasslands and sal forest. The use of grassland was, however, at its seasonal low, which was not surprising since many of the grasslands were periodically inundated for periods of 1–2 weeks, and ungulates moved to higher, drier ground in the forests.

DISCUSSION.—The preference of tigers for grassland and riverine forest is undoubtedly related to the fact that these habitats, in contrast to sal forest, characteristically have all the requisites for the tiger's life style; namely dense vegetation, widely distributed permanent water sources, and a higher prey density and biomass. The greatest ungulate biomasses are attained where forest and grassland or alluvial plain are interspersed to create a mosaic of cover types (Eisenberg and Lockhart, 1972), as well as more "edge effect" (Leopold, 1933). Seidensticker (1976b) estimated prey density and biomass in Chitawan's grassland/riverine forest to be about four and two times greater, respectively, than in sal forest. Similar differences in numerical density and biomass between these habitat types were reported by Tamang (1979).

The habitat superiority of grassland/riverine forest is clearly evident in the kill data; only 5 of 45 (11%) wild ungulate kills were found in sal forest, where tigers were located 13%–31% of the time. Admittedly we were less likely to locate tigers in sal forest, but the magnitude of this difference suggests the relative importance of certain habitat characteristics on prey availability and consequently on hunting success.

Seasonal differences in habitat use for the most part can be explained by changes in the conditions conducive to making kills. The tiger's use of tall grass areas along permanent streams would afford it cover for stalk and/or ambush, which during the hot season may be at premium due to burning. In addition, ungulates need to drink more often at this time of year (Schaller, 1967; Berwick, 1974; Dinerstein, 1980), which could conceivably improve these areas as hunting sites. Of nine chital and hog deer killed in the hot season, when the grasslands had been burned, seven were found in dense cover along streams. As the grasslands provide little cover at this time, the kills were made either at the edge of dense vegetation or at night. Daytime stalking requires suitable cover, which for the lion is a combination of terrain and/or vegetation measuring at least 41 cm in height (Elliott, et al., 1977). A similar combination of vegetation/terrain may be necessary for the tiger, as one was observed stalking four chital at mid-morning in an open grass area, where the cover was only 30 cm high, and it was unsuccessful. The general absence of suitable cover in the hot season may be the reason tigers show significantly less daytime activity at that time (Figure 17). Hunting at night may be more successful because the constraints of cover are reduced.

Differential use of habitats may also be related to changes in vulnerability of prey. Chital, for example, are usually seen in groups of six to ten individuals, but feeding aggregations of 50–200 animals are not unusual on open burned grasslands (Schaller, 1967; Tamang, 1979; Dinerstein, 1980). Hog deer are also seen in larger groups (five to twenty individuals) on open grass areas after burning, whereas the average group size is about two (Seidensticker, 1976b; Tamang, 1979; Dinerstein, 1980). Large groups form in open habitats for the likely benefit of reduced predation (Jarman, 1974), and while these observations support the theory, it was not known if a greater percentage of chital and hog deer were taken when the grass had again grown high. The reduction of cover and corresponding change in vulnerability of prey is, however, suggested from baiting records. McDougal (1979) observed that the peak use (51%) of bait sites in Chitawan occurred from February through April, the time of least cover. Relatively more sambar, an essentially solitary forest animal, were killed when cover was reduced on the grasslands, but it is unclear if this is related to increased vulnerability or other factors. Sample sizes were too small to indicate seasonal differences in prey selection, although sambar are highly preferred prey (Tamang, 1979). Additional aspects of prey selection are discussed in "Feeding Ecology."

It is interesting that the sexes differed significantly in their seasonal use of habitats, as there was no significant seasonal difference in their activity patterns, and the limited data on prey selection show no marked difference in size of prey taken. A separation by habitat use may be an adaptation to reduce conflict for food, as this could effectively increase a female's chances of successfully rearing her and quite probably the male's offspring. If this is true, females should receive preferential use of the "best" habitats, but there is no data available to show this. Such a difference may be related to not only seasonal use of habitats but possibly even to the time certain habitats are used. Continuous monitoring of individuals, coupled with information on variation in prey availability by habitat, are needed to show whether such subtle differences exist.

While seasonal changes in habitat components appear to affect hunting strategies, this variability has broader biological implications. That tigers have been observed lying in water during the hot season (Schaller, 1967; Singh, 1973; Sankhala, 1977) strongly suggests its importance in thermoregulation at that time. The water economy of wild carnivores is not well known, but lions do not require water every day (Schaller, 1972; Eloff, 1973a), and Hamilton (1976) believed that this is also true of leopards. Domestic cats can survive perfectly well on a diet of beef and fish alone (Schmidt-Nielsen, 1964), but under heat stress water is needed for evaporative cooling, and dietary water is insufficient. The tiger's frequent and close association with water in the hot season is not apparent at other times of the year, which suggests this is a behavioral thermo-regulatory response. If this is so, the seasonal availability or distribution of water could influence spacing patterns, both by affecting the tiger directly or indirectly through the dispersion of prey. Preliminary observations in Palamau Reserve, India, indicate that whereas ungulates usually left the area in summer, when water was scarce, they now remain following the provision of year-round water in check dams. Tiger density also appears to have increased (Sinha, 1979b). In Sri Lanka, Eisenberg and Lockhart (1972) have shown that the distribution of forage and water influences ungulate density, and thereby leopard density. Where ungulates are concentrated around a few large, permanent water holes, leopards have relatively small, mutually exclusive ranges, and their intraspecific spacing system effectively limits their density (Muckenhirn and Eisenberg, 1973). The effect of fluctuations in availability and distribution of limited resources on temporal and spatial utilization patterns has also been suggested or demonstrated in a variety of birds and mammals (Crook, 1965; Eisenberg, et al. 1972; Brown and Orians, 1970; Gill and Wolf, 1975; Waser, 1976; Clutton-Brock and Harvey, 1977). The dispersion of resources in relation to the spatial system of tigers is considered in more detail in the section "Home Ranges."

Movements and Home Ranges

METHODS AND DEFINITIONS

An index of movement was derived by measuring the straight-line distance between the first location of radio-tagged individuals on consecutive days. Only data from days when tigers had changed locations were included. An animal was considered to have moved if, when relocated, its position had changed by at least 135 m.

An estimate of how far tigers travel in a day was obtained by repeatedly locating tagged animals throughout the night, which is their major movement period. Total distance travelled is the sum of the straight-line distances between consecutive locations.

An estimate of how frequently tigers use roads and how far they travel on them was obtained by routinely searching for tracks on a 5.0 km section of the park road. Since this information may have value as a census technique, the estimated number of tigers using the area (based on tracks) was compared with the corresponding number of tagged individuals located in the same area.

Home range size was calculated by the "minimum area" of Mohr (1947), which is the area of the polygon formed by connecting all the outermost locations, except those judged to be forays. The size of the area used, as calculated by this method, is dependent on the number of locations. To ascertain what constituted an adequate sample, I utilized a cumulative area curve (Odum and Kuenzler, 1955). As the number of locations increase, home range size increases towards an asymptotic limit; at this point range size is 'maximum' and the number of locations considered adequate.

A tiger that appeared permanently restricted to a specific area is termed a resident, and the area it uses is termed a home range. These ranges also appear to be territories (Wilson, 1975:256), as will be shown later. Movements outside an animal's home range are labelled forays and are not considered part of the home range. While subadults may reside within their natal areas for extended periods of time, they are not considered to have established ranges. There is another segment of the population, referred to as transients (Schaller, 1967), which are often young adults occupying marginal habitats; no information is available to indicate whether transients have home ranges.

MOVEMENTS

Tigers were found in a different place on 72 percent (range 70%–76%) of all consecutive location days (N=503, data from five tigers pooled). They were also not commonly found in previous locations. An animal was located in a specific grid square (1.8 ha) only once about 60–76% of the time (Figure 19). Since most locations were obtained during the daytime, when tigers are least active, it does indicate that individuals normally choose a different rest site each day, and these were well distributed over their ranges. Several specific rest sites were known to have been used (not simultaneously) by more than one animal, and these were typically tall grass areas along permanent streams.

The mean linear distance moved between consecutive daily locations was 2.0 km (N=362) with considerable variation among individuals (Table 9). Individuals ranged from 1.4 to 2.8 km and their maxima were from 3.8 to 10.9 km. An adult male (105) moved significantly ($P<0.05$) farther than all other tigers on a day-to-day basis, averaging 2.8 km between locations. The subadult male (104) did not move significantly farther than his sister (103), but she moved significantly farther as an adult than as a subadult. One adult female (106) moved significantly less than all other tigers, averaging only 1.4 km between daily locations; this was probably related to her having dependent young. The effect of young on the movements of females is evident from data on another tigress. When female 101 had 1-day- to 2-month-old young, the mean linear distance moved between consecutive daily locations was 0.7 km (range, 0.2 to 1.7 km, N=10); on most days during this 2-month period 101 was with her litter when first located. When 101 had a different litter of 6-10-month-old young, the mean linear distance moved between consecutive daily locations was 1.0 km (range, 0.2 to 2.0 km, Seidensticker, 1976a).

There is a positive relationship between the mean linear distance moved between consecutive daily locations and home range size, and the correlation approached significance ($r^2=0.64$, $P\leq0.05$). Females with small young had the smallest ranges and moved the shortest distances between daily locations; females without young had larger ranges and moved farther, and the adult male (105) had the largest range and moved significantly farther between daily locations. Similar observations were recorded for adult mountain lions (Seidensticker, et al., 1973) and leopards (Hamilton, 1976).

While the linear distance between daily locations is useful as an index of movement and range size, it underestimates the distances actually travelled. Estimates of how far tigers travelled in a 24-hour period were two to 15 times greater than the corresponding linear distance between daily locations (Table 10), and there was no significant correlation between them (Spearman rank correlation, $r_s=0.535$, $P>0.05$). To what extent these estimates of distance travelled per day (Table 10) represent actual distance travelled is uncertain because of accuracy limitations in the tracking system (i.e., short movements are not detectable) and the length of the sampling interval. It was apparent, however, that females did not often move rapidly or continuously between distant points within their ranges. The average straight-line distance moved between hourly nighttime locations was 0.7 km (range, 0.2 to 1.2 km/hr, N=40). While short zigzag movements would obviously increase the distance travelled, it seems unlikely that females would have travelled more

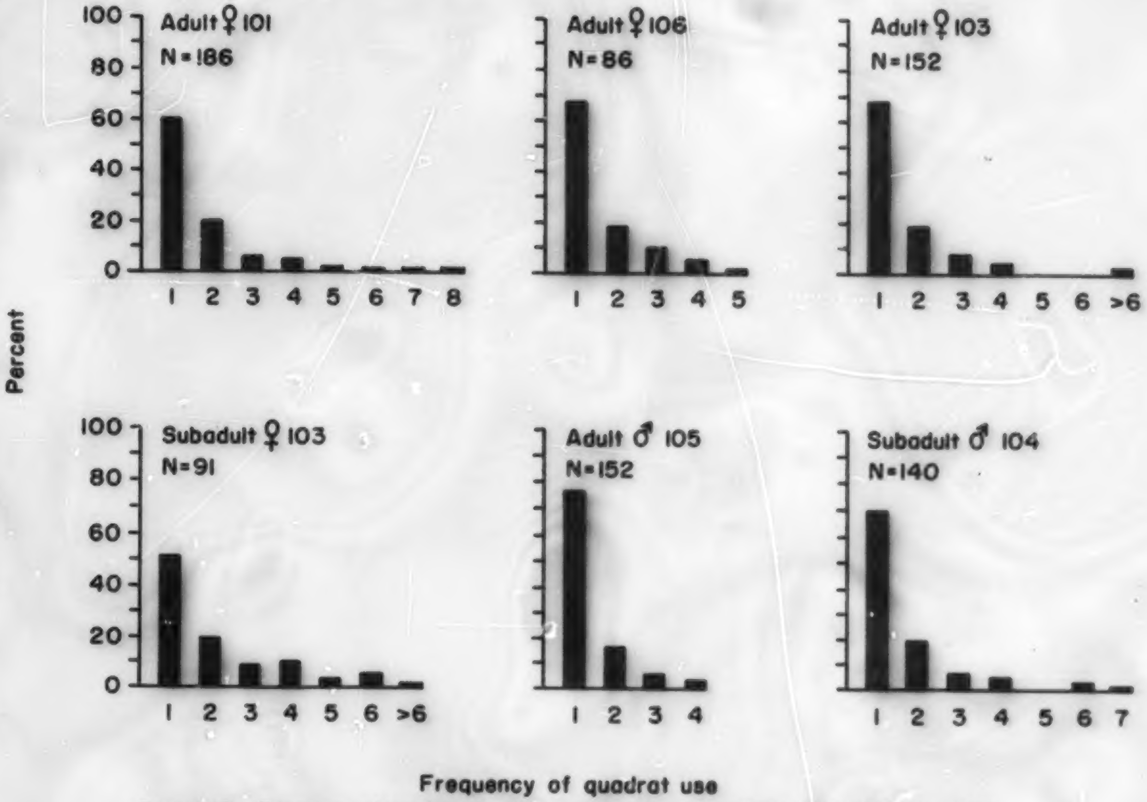


FIGURE 19.—Frequency of quadrat use (N = total number of quadrats (each 1.8 ha) in which animal was located, excluding those when females had small (non-following) young; for example, female 101 was located in 186 quadrats, 60% of which she was found in only once, 20% twice, 7% three times, etc.).

TABLE 9.—Linear distance between locations of tagged tigers on consecutive days (N = number of times located on 2 consecutive days; s.e. = standard error)

Tiger no.	*N*	*Mean distance ± s.e. (km)*	*Maximum distance (km)*
101 Adult F	97	2.2 ±0.1	5.6
103 Subadult F	61	1.8 ±0.1	7.1
103 Adult F	77	2.2 ±0.1	6.0
104 Subadult M	58	1.8 ±0.1	8.0
105 Adult M	41	2.8 ±0.3	10.9
106 Adult F	28	1.4 ±0.2	3.8

than twice the distance indicated by hourly radio-locations, or about 10–20 km/night. Location data on males were too few to indicate the extent of their daily travels, although given their larger ranges it may be anticipated that they would move farther.

Movement data showed that while boundaries are not patrolled, home ranges are well covered. Resident females visited most parts of their ranges at intervals (minimum) of a few days to two weeks, but their movements were not predictable (Figures 20 and 21). On some occasions they crossed their ranges in a single night, while at other times they remained in a portion of it for several days. Females were located most frequently in those parts of their ranges where prey density and biomass were highest, but 13%–26% of locations (Table 8) were in "poor" game areas where few kills were recorded.

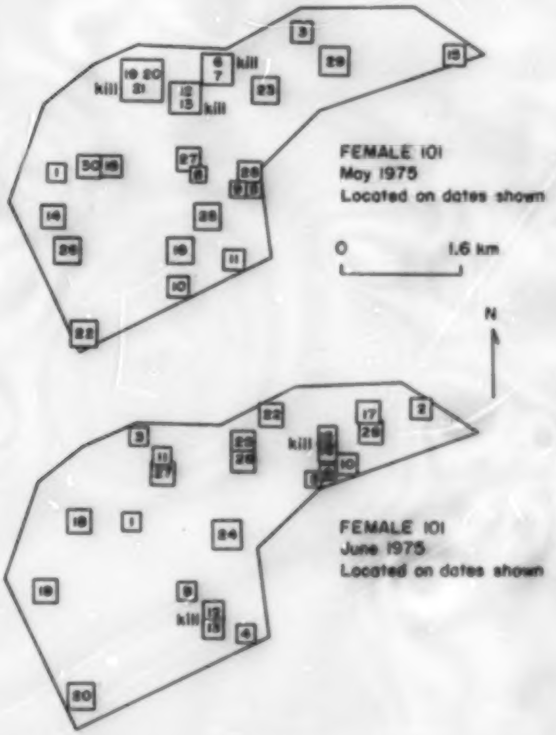


FIGURE 20.—Movements of resident female 101 in relation to her home range (radio-located at approximate points on dates shown).

Whether resident males visit most parts of their ranges as frequently as females was not known as precisely. The ranges of two resident males (102, 105) were comparatively large (60–75 km^2) and our range of mobility was often restricted, so it was only possible to regularly monitor a portion of one male's range. From January through May (1975, 1976) the eastern one-third (20 km^2) of male 105's range was searched almost daily; the longest interval between searches was two days (Table 11). In 1975 male 105 was located in the eastern one-third of his range 33% of the time; in 1976 this decreased to 19%, a significant difference (X^2=4.621, 1df, $P<0.05$). There was, however, no significant yearly difference in the average number of monthly visits to this part of his range (4.2 vs 3.6 visits/mo; Table 12), but in 1976 his average length of stay was significantly shorter (2.1 vs 1.4 days), and the mean interval between visits was significantly longer (5.2 vs 6.8 days).

Male 105 typically visited the eastern one-third of his range frequently, stayed a short time, and returned at relatively short intervals. Whether he used the other portions of his range in the same manner I was unable to determine, but data collected in May 1975 suggest that he did. No long sequence of movements was obtained, but in one 10-day period he was in the eastern one-third of his range for two days, then in the western third for two days, back in the eastern third for three days, and then in the middle one-third for three days. During this month he was located on 21 days: 11 days in the eastern one-third, five days in the middle one-third, and five days in the western one-third. He was not found in the eastern portion on another eight days. Assuming he divided these eight days equally between the other portions of his range, then each one-third

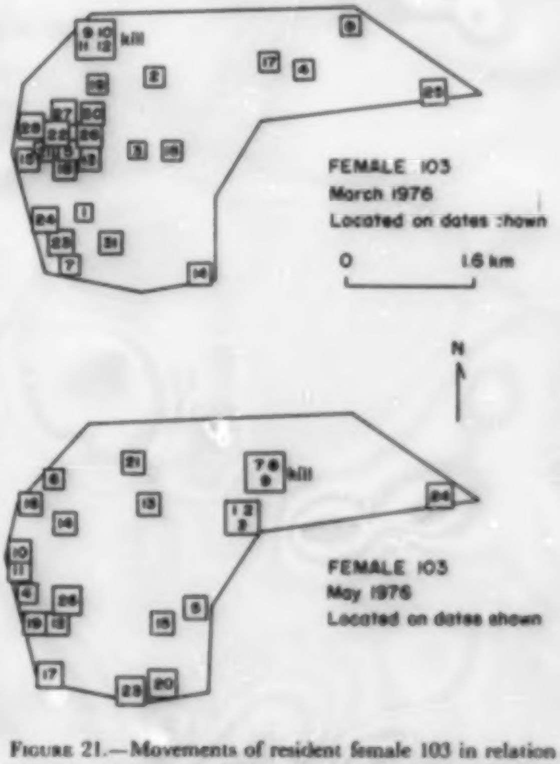


FIGURE 21.—Movements of resident female 103 in relation to her home range (radio-located at approximate points on dates shown).

TABLE 10.—Comparisons of linear distances between consecutive daily locations with corresponding estimates of total distances traveled in 24-hour period, as determined by repeated locations (N = number of locations; N minus two = number of night locations; interval between night locations was 0.5 to 3.0 hours)

Tiger no.	*Dates*	*N*	*Linear distance between consecutive daily locations (km)*	*Estimate of total distances traveled (km)*
103	14-15 Apr 75	8	3.3	9.6
103	20-12 Apr 75	7	0.8	6.9
103	31 Jan. - 1 Feb 76	9	4.4	8.5
103	11-12 Apr 76	10	0.3	4.4
103	12-13 Apr 76	11	0.8	3.8
103	19-20 Apr 76	12	1.7	4.3
101	12-13 Apr 76	12	0.5	5.9
101	10-11 May 76	6	1.2	8.6
101	19-20 May 76	12	1.4	5.5
104	28-29 Apr 75	7	1.2	4.8
105	11-12 Apr 76	6	0.5	2.7

TABLE 11.—Estimate of time tiger 105 spent in eastern one-third of his home range

No. of days area was searched (percent of possible days)	*No. of days tiger was radio-located*	*No. of days tiger was radio-located in eastern one-third of range*	*Percent of time in eastern one-third of range*
136 (Jan–May 75) (90%)	71	45	33 (45/136)
134 (Jan–May 76) (88%)	52	25	19 (25/134)

TABLE 12.—Estimates of frequency, duration, and interval of visits of tiger 105 to eastern one-third of his home range (N = number of visits or intervals)

Month	*Visits/mo.*	*Mean duration of visit (days, range)*	*Mean interval between visits (days, range)*
Jan 1975	6	2.0 (1-4)	3.8 (1-7) (N=5)
Feb	3	1.7 (1-3)	7.7 (5-11) (N=3)
Mar	4	1.5 (1-2)	5.3 (2-11) (N=4)
Apr	3	3.6 (1-5)	6.3 (4-8) (N=3)
May	5	2.2 (1-3)	4.6 (2-8) (N=5)
Totals	4.2 (N=21)	2.1 (1-5)	5.2 (1-11) (N=20)
Jan 1976	4	1.3 (1-2)	8.7 (5-13) (N=3)
Feb	2	1.0	11.5 (8-15) (N=2)
Mar	4	1.3 (1-2)	6.8 (4-12) (N=4)
Apr	6	1.3 (1-2)	4.2 (1-12) (N=6)
May	2	2.0	7.0 (5-9) (N=2)
Totals	3.6 (N=18)	1.4 (1-2)	6.8 (1-15) (N=17)

was used about equally. J.L.D. Smith (1978) reported that 105 showed a similar pattern of movement, even after he doubled the size of his range; indicating that 105 seldom spends much time in one area and few parts of his range are likely to remain unvisited for extended periods.

Tigers used the park road and many trails to travel about and/or to hunt different areas within their ranges. A 5.0 km section of this road was searched on 390 days and on 170 days (44%) tracks of at least one tiger were recorded. By comparison, leopard tracks were found on 38 days (10%). During the period of data collection two to four tigers and two to four leopards used the area, indicating that leopards travelled the road much less frequently than did tigers. Leopards tended also to travel shorter distances on the road, rarely were tracks followed for more than 400 m; the longest recorded was 2.4 km. In contrast, on 52 days tiger tracks were followed on the road for distances of 1.2 km to 5.0 km. On one occasion the tracks of the resident male (105) were followed on the road for 13.5 km. In this instance he essentially travelled the length of his range, and there was no indication he rested enroute. Another male's tracks were followed on the road for 9.1 km, and here again the animal did not appear to have rested. Tracks of an adult female were followed on the road and trails for 8.6 km. Male 105 has since expanded his range, and J.L.D. Smith (1978) reported that by utilizing the east-west park road, 105 has travelled 20.5 km in less than 12 hours, and on another occasion 16.0 km in 7.5 hours. J.L.D. Smith (1978, in prep.) has suggested that the park road facilitates rapid and directional travel through the area and partially contributes to the ease with which 105 can cover his expanded range.

There are few topographical features in the park to obstruct tiger movements, and, except at peak flows, even large rivers are crossed. Animals occasionally travelled ridge lines, or followed trails along the base of slopes, but paths beside or in river beds and ravines seem to be preferred. The same trails and river crossings were used at different times by several tigers and some routes appeared to be more intensively used, but there was no rigid network of pathways, as described by Leyhausen (1965) for the house cat (*Felis catus*). Different tigers used the road and associated trails irregularly and at variable frequencies. For example, an individual would use the same trail on two or three consecutive nights and then not again for several days, even though it remained in the vicinity.

It was not usually possible to relate tracks to specific individuals except in cases where the animal had an unusual track pattern and we were able to follow the tracks over some distance to observe the variation related to changes in substrate. Tracks of adult males are, however, much larger than those of females, thus providing an indirect means of census. For example, on 37 days, tracks of a large male were observed on the road in the northeast part of the park, and on 35 (95%) of those days, male 105 was located in the same vicinity. He was, however, located in this area on an additional 35 days when no tracks of a large male were observed. Thus, a census based only on tracks would tend to underestimate the number of tigers using an area. This is further illustrated in Table 13, which shows the comparison between the number of tigers in an area based on tracks and the corresponding number of tagged tigers located in this area. The comparison suggests that a census based only on tracks is fairly reliable, but it should be noted that these observations were limited to one relatively small area and the tracks of the four animals (two males, two females) using this area could be separated by sex and one female had an unusual track pattern. In addition, no other tigers were known to use this area on a regular basis. Another factor to consider is the probability of not finding tracks when an animal is present. Females may be with young or an animal may have a large kill, and movement would be restricted, or as noted above, an animal could be in an area without indicating its presence by tracks. In this comparison, no tracks were found on 41 days when one or more tigers were located in the area (Table 13).

Home Ranges

The home range sizes of resident females in the northeast section of the park were relatively small, about 16–17 km^2 (Table 14). An examination of the cumulative-area curves (Figure 22) shows that female ranges were limited in size, and that "maximum" range size was usually reached by the time an individual had been located on 45 days.

Table 13.—Comparison of number of tigers in area based on tracks and radio-location data (Mar–May in 1975 and 1976)

Estimate of no. of tigers in area based on tracks on 5.0 km section of road	*No. of days*	*No. of tigers radio-located in area*	*No. of days*	*Percent agreement between tracks and radio-location data*
0	79	0	38	48
		1	29	
		2	11	
		3	1	
		0	3	
1	55	1	38	69
		2	12	
		3	2	
		1	3	
2	25	2	18	72
		[illegible]	4	
3	6	[illegible]	5	83
		4	1	
4	2	4	2	100
Total	167			

Range sizes of females varied seasonally, tending to be largest in the hot season and smallest in the wet season, when only 60%–70% of the total yearly home range was utilized. Further range contractions and expansions are associated with birth and the raising of young. The area traversed by female 101 did not diminish appreciably in the periods before her young were born, but the births were marked by an obvious reduction in the extent of her travels (Table 15). Female 106 also confined her movements to a relatively small

Table 15.—Range sizes of female 101 before and after birth of two litters

Date	*No. of locations*	*Home range (km^2)*
3-31 Mar 75	25	6.3
4-15 Apr 75[a]	16	0.6
16-31 Apr 75	36	6.4
1-31 May 75	57	9.6
4-30 Nov 75	9	11.2
2-13 Dec 75	9	7.2
14-29 Dec 75[b]	34	1.1
2-30 Jan 76	30	3.3
2-29 Feb 76	11	1.6

[a] Young born about 4 Apr 75, died in fire on 15 Apr.

[b] Young born about 14 Dec 75.

Table 14.—Size of seasonal and yearly total home ranges (km^2) of tigers as calculated by minimum area method (size of areas used by two subadults also included; NA = radio tagged but data not adequate for home range determination)

Tiger no.	*Cool season*		*Hot season*		*Wet season*		*Yearly total*	
	1974–1975	*1975–1976*	*1975*	*1976*	*1975*	*1976*	*1975*	*1976*
103 Subadult F	10.3		14.8		5.3		19.7	
103 Adult F		13.0		16.5		10.9		16.5
101 Adult F	–	11.2[a]	11.3	–	8.9	–	16.4	–
106 Adult F	NA	10.4	3.0[b]	12.8	11.1	–	17.7	12.8[c]
104 Subadult M	23.2	–	14.4	–	31.9	–	44.7	–
104 Adult M	NA	42.5	30.0	27.3	28.0	–	48.0	60.2

[a] Had young in mid-December; lost home range in February.

[b] May have had young.

[c] Died in July.

area during the hot season (1975, Table 14), suggesting she might have had young at that time. This was not confirmed but 10 months later she was observed with two large cubs. There is a gradual increase in range size as the young get older, but the effect of young on a female's movements is evident for some time. For example, compare (Figure 22) range sizes of 101 with small young, with 6-10-month-old young, and without young. J.L.D. Smith's (1978) observations on two tigresses show the same pattern; as their young went from about four to 16 months of age their ranges changed from 10.5 km^2 and 11.5 km^2 to 20.4 km^2 and 19.0 km^2, respectively. Females with dependent young are obviously most restricted in their movements during the young's first year of life and least restricted after the young have reached independence.

The home range size of the resident male (105) in the northeast section of the park was about 60 km^2 (Table 14). During 1975 he covered an area of at least 48 km^2, but the full extent of his range had not been determined as indicated by the upward trend of the cumulative-area curve (Figure 22). Since this study was terminated 105 has expanded his range to where he is covering about 100 km^2 (J.L.D. Smith, pers. comm.). The range size of another resident male (102) was approximately 72 km^2 (based on 16 radio-locations, and observations by McDougal, 1977).

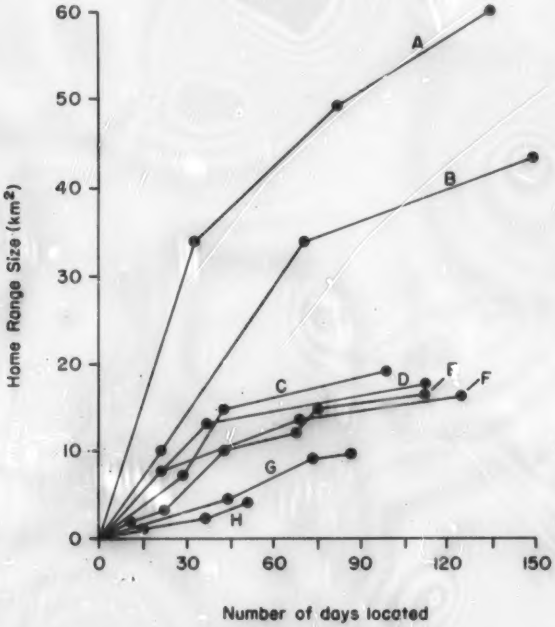


FIGURE 22.—Cumulative area curves for home ranges of adult male 105 (A), subadult male 104 (B), subadult female 103 (C), adult female 106 (D), adult female 103 (E), adult female 101 with no cubs (F), adult female with 6- to 10-month-old cubs (G), and adult female 101 with 1-day- to 2-month-old cubs (H). (Data on G from Seidensticker, 1976a.)

Seasonal variations in 105's range size (Table 14) do not show the full extent of his travels, but as the number of locations in each period was about the same, the differences probably indicate seasonal trends. A larger proportion of the total yearly range is covered in the cool season and range size is smallest during the wet season.

The cumulative area used by the subadult male (104) increased in size over the 10 months he was radio-tracked (Figure 22). In the first month after capture he was not located outside his natal area, but in the following months he was found outside of it on many occasions, sometimes as far away as 10 km. Prior to his apparent dispersal, 104 ranged over an area of at least 45 km^2 (Table 14); this included his mother's (101) range and that of the resident male (Figure 23). By comparison, his sister (103) during the same time period ranged over an area of about 20 km^2, most of which was within their mother's range (Figure 23). Males tend to travel independently earlier than females (Schaller, 1967; McDougal, 1977), and the above differences also suggest that subadult males wander more extensively.

RELATIVE STABILITY OF HOME RANGES

Home ranges of resident animals appear to be stable, at least for several years. Tigress 101 is known to have occupied essentially the same area for 27 months; she established a new range in 1976, and has remained there for the last three years (J.L.D. Smith, pers. comm.). Her former range has been occupied by her daughter (103) for the last three years (J.L.D. Smith, pers. comm.). Another tigress (106) was, prior to her death, a resident in a different area for at least 17 months; her former range has been occupied by another tigress for almost three years (J.L.D. Smith, pers. comm.). An adult female (107) tagged in early 1976 has remained in essentially the same area for the last 3.5 years (J.L.D. Smith, pers. comm.); and at the western end of the park, several tigresses have occupied their respective ranges for three to eight years (McDougal, pers. comm.). Unless there are some unexpected changes, many of these females may well be residents for several more years.

A similar situation exists for the resident males, although some changes have occurred. In the northeast part of the park, male 105 was the resident for at least 18 months, and he continued to be for the next three years (J.L.D. Smith, pers. comm.), but he has since expanded his range. The resident male (102) at the western end was, prior to his death, the resident in that area for 30 months (McDougal, 1977).

ACQUISITION AND EXPANSION OF HOME RANGES OF MALES

Male 102 disappeared in August 1976 and his remains were later found along the park boundary (Smith and Tamang, 1977). On 5 September 1976, less than a month after 102's disappearance, male 105 had expanded his range to include a portion of 102's former area, and over the next several months he gradually moved westward (McDougal, 1977). At about the same time another adult male established himself in the other part of 102's former range (J.L.D. Smith, 1978). This indicates that as vacancies occur the space will be occupied by other adult males, although entire ranges may not be acquired intact but involve a reshuffling of space.

ACQUISITION AND LOSS OF HOME RANGES OF FEMALES

In the northeast quarter of the park there was a range shift in early 1976 involving tigresses 101 and 103; 103 is the daughter of 101. This change involved a sequence of events. From January 1975 to early May 1975 female 103, though independent, restricted her movements to her mother's range (Figure 23). No aggression was noted between these females during this time, but in early May 103 shifted her activities to a small island just outside her mother's range. She was estimated to be two years old at this time and not yet sexually mature. During the next nine months (May 1975–February 1976) 103 was found in her mother's range on only seven days, all of which were along the periphery of 101's range (Figure 24). Her activities were restricted primarily to the island and a thinly forested area north of the Rapti River until early February 1976.

In mid-December (1975) 101 had another litter of cubs in almost the same place as a previous litter, which was lost in a grass fire (April 1975), and her movements (Figure 24B,C) centered on this area until early February 1976. The annual cutting and burning of grass by villagers began in the park in mid-January 1976, and during the last week of January 101 had on four occasions charged and threatened villagers who were cutting grass near the den site. Following these encounters, 101 shifted her activities and presumably the young as well to another part of her range for the month of February (Figure 24D). During 101's absence her now sexually mature daughter (103, see "Social Interactions") began using the other portions of her range and apparently gained exclusive rights to these areas (Figure 25). Number 101 made a few excursions back into her old area in March and April (1976) but by May 103 was occupying about 90% of her mother's former range (Figure 25). The movements of 103 from May through August 1976 clearly show the total appropriation of 101's former range (Figure 26).

Number 103 is known to have occupied essentially the same area over the next three years and had two litters in the same area her mother had used as a den site (J.L.D. Smith, pers. comm.).

Following this incident the movements of 101 were irregular, and, based on her close association with the resident male (105) in March and April 1976, it also appeared that she lost her cubs. Females with small cubs do not usually associate with adult males (McDougal, 1977; Panwar, 1979). Number 101 continued to move about in

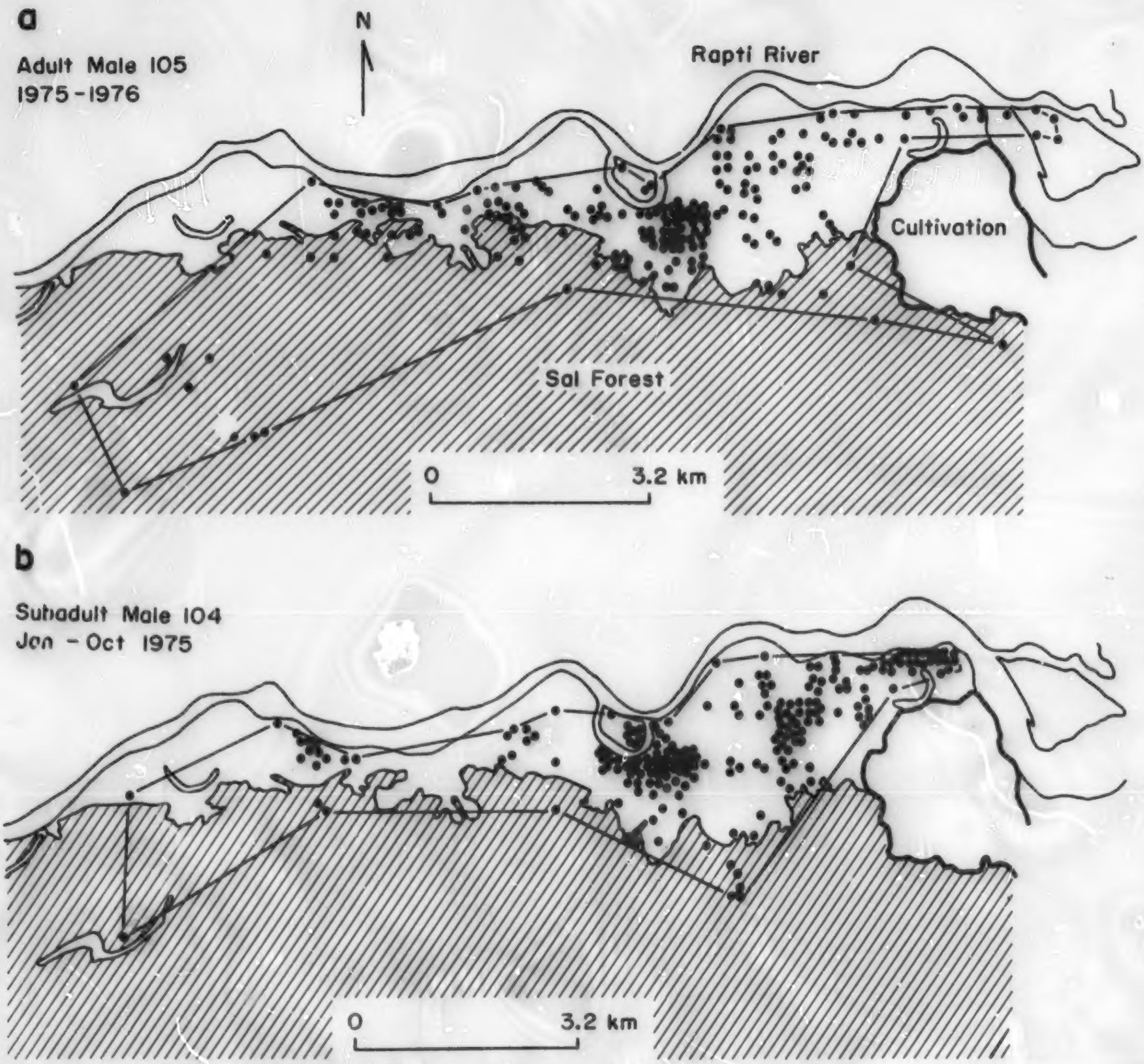
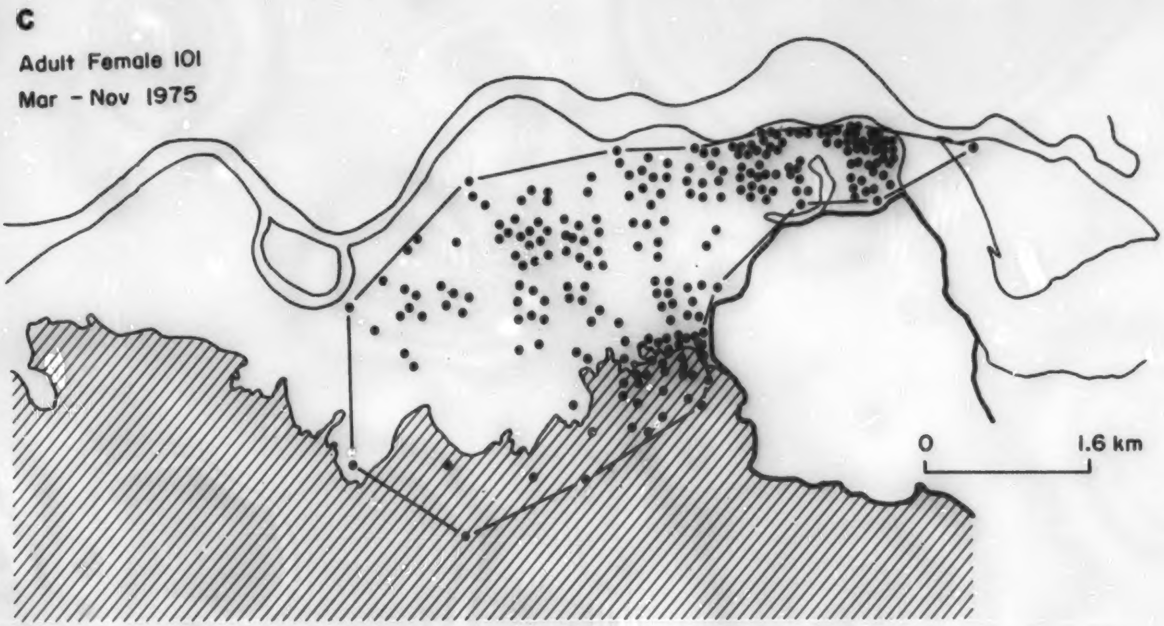

a
Adult Male 105
1975-1976
N
Rapti River
Cultivation
Sal Forest
0
3.2 km
b
Subadult Male 104
Jan - Oct 1975
0
3.2 km

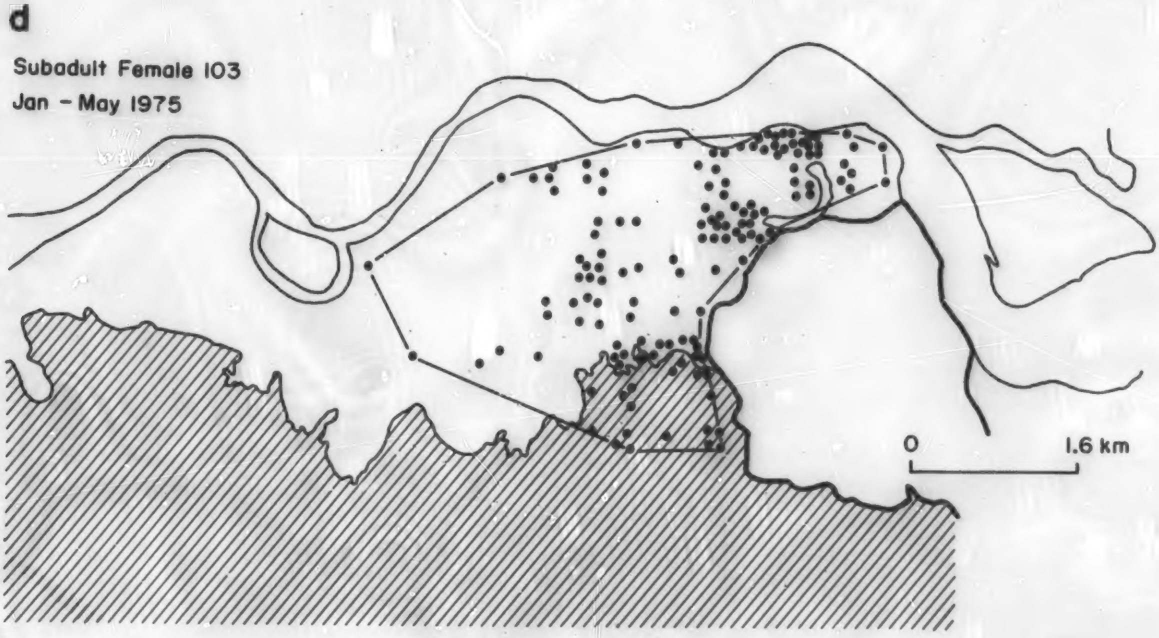
FIGURE 23.—Home ranges: *a*, adult male 105 (in relation to *b*); *b*, subadult male 104; *c*, adult female 101 (in relation to *d*); *d*, subadult female 103. (Note larger male ranges; solid circles = radio locations.)

areas along the periphery of 103's range in March–May, but she also went on forays to other areas of the park. In May 101 was captured in the home range of another resident female (106), and she was not accompanied by young. This marked the first time in 14 consecutive months of tracking that 101 was located in 106's range, and in the same time period 106 was never located in 101's range. This study was terminated in August 1976, but since then 101 has established a new home range, adjacent to 103's, and for the next three years she remained in this area and produced another litter (J.L.D. Smith, pers. comm.).

LAND TENURE SYSTEM

The land tenure system of tigers is apparently based on prior rights. No neighboring resident or


c
Adult Female 101
Mar - Nov 1975
0
1.6 km


d
Subadult Female 103
Jan - May 1975
0
1.6 km

transient settled permanently in an area already occupied by a resident, indicating that occupancy confers rights to an area. Young tigers reared in Chitawan did not settle there, but dispersed to other areas. One collared male, for example, was sighted by several different woodsmen (pers. comm.) about 240 km east of Chitawan. A female (103) reared in the park later established a home

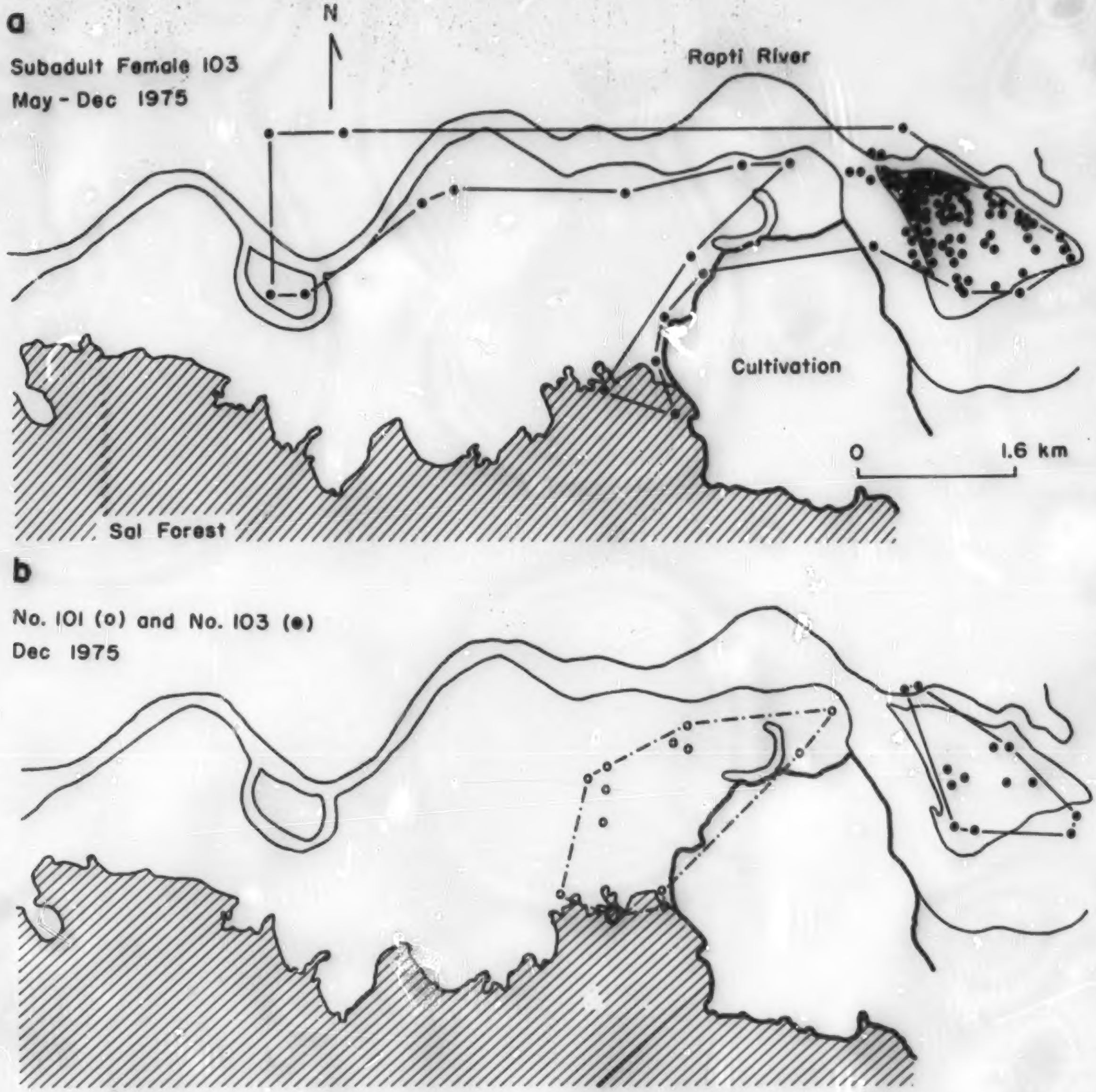
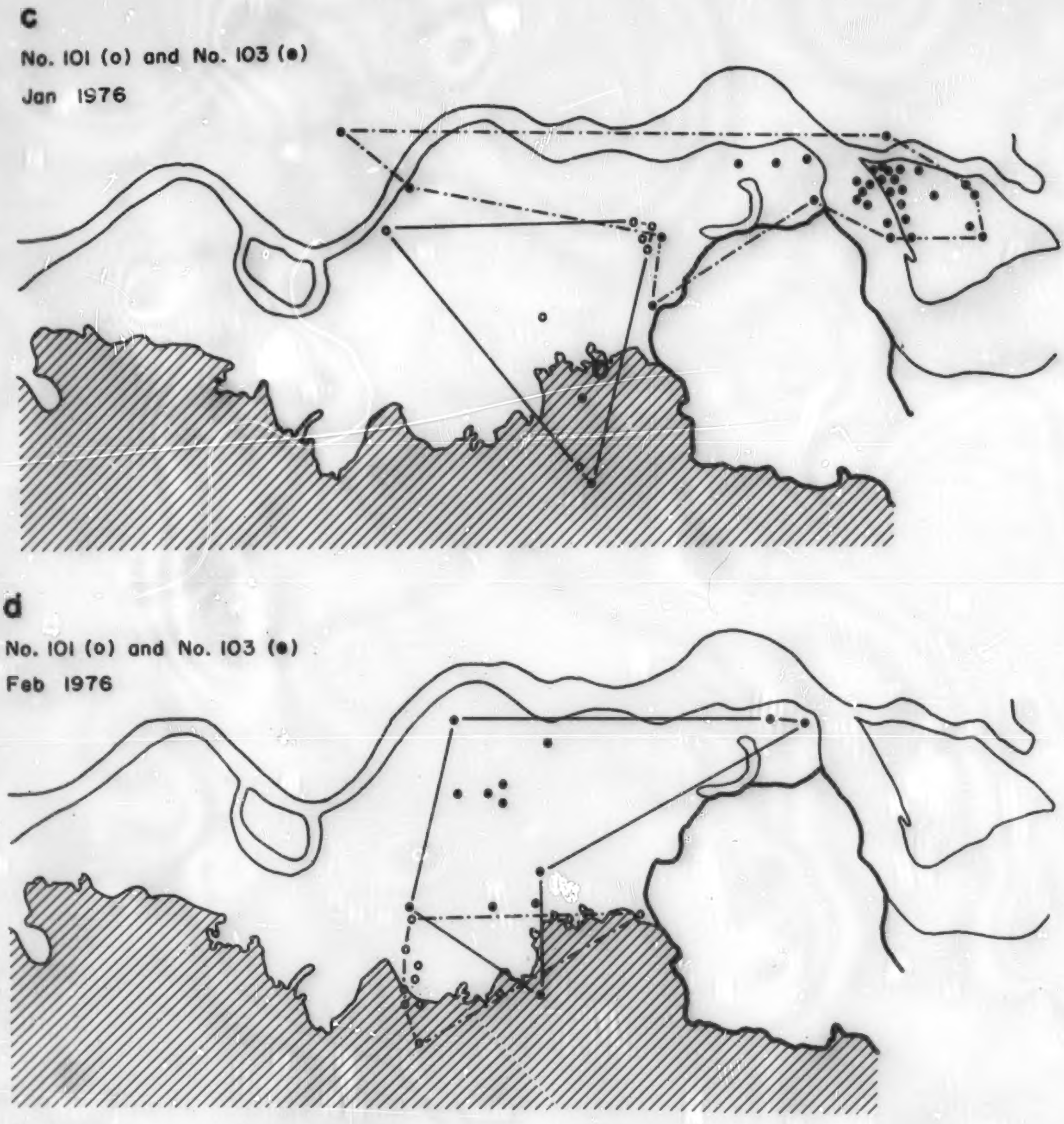

a
Subadult Female 103
May - Dec 1975
N
Rapti River
Cultivation
0
1.6 km
Sal Forest
b
No. 101 (o) and No. 103 (●)
Dec 1975

FIGURE 24.—Areas used by female tigers 101 and 103: *a*, subadult 103, May–Nov 1975, after leaving mother's (101) home range; *b*, range of movement for Dec 1975; *c*, range of movement for Jan 1976; *d*, range for Feb 1976. (Large open circle = location where 101 gave birth in Dec 1975; circles = radio locations.)

range there, but only when a vacancy occurred. All observed changes in resident tiger home ranges and occupancy were in response to either the death or movements of residents. For example, portions of 102's range were appropriated by two males after 102's death, and after female 106 died her range was occupied by another female. A vacancy created by the death or movement of


c
No. 101 (o) and No. 103 (●)
Jan 1976
d
No. 101 (o) and No. 103 (●)
Feb 1976

a male does not create an opening for a female, or vice versa; their land tenure systems are essentially independent.

The home ranges of resident tigers also appeared to be territories, in the sense that both males and females occupied areas that were not shared with neighboring like-sexed adults. There was no overlap in the ranges of two resident males (102, 105), but each of their ranges overlapped those of several females (Figure 27). The ranges

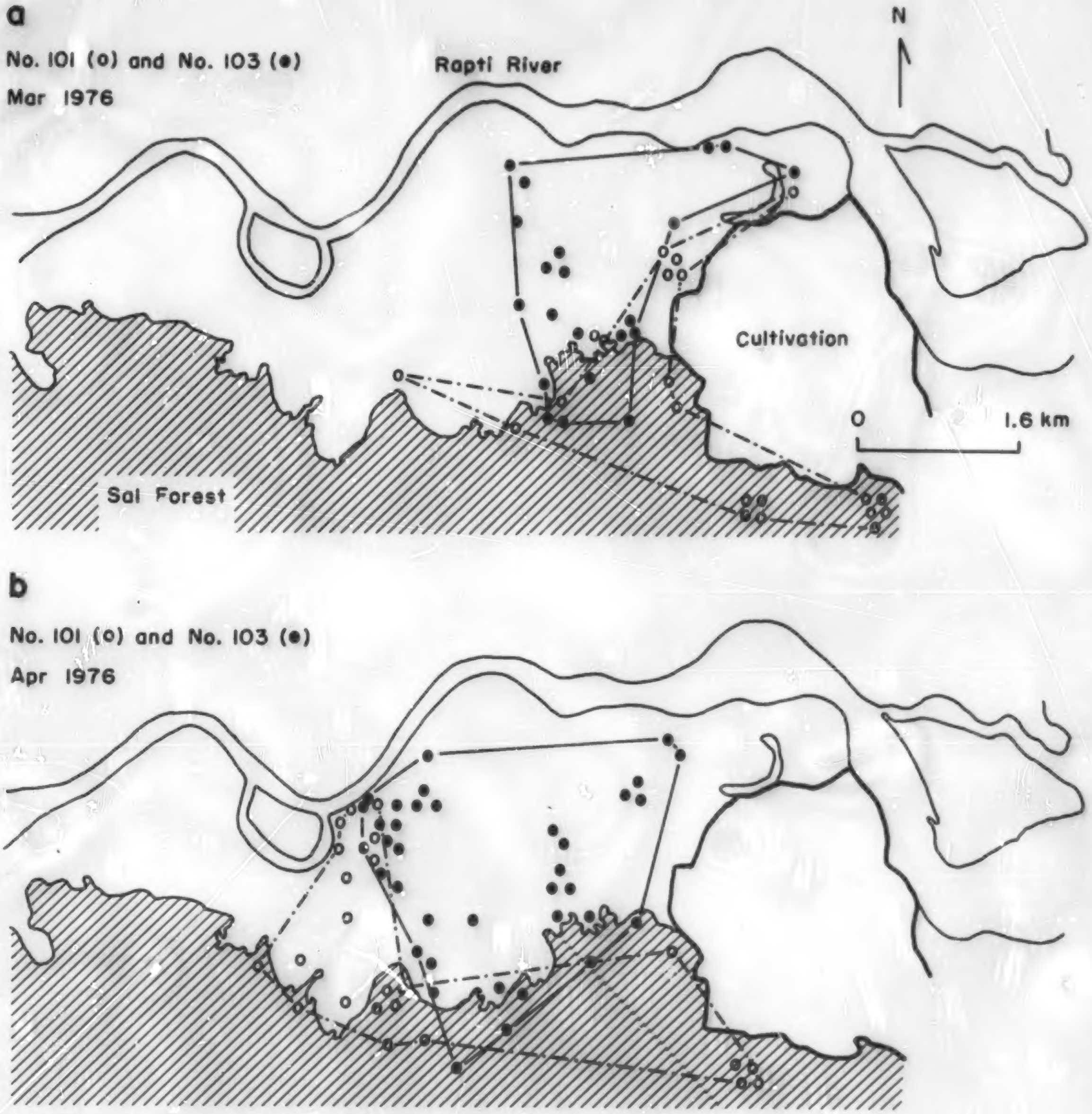
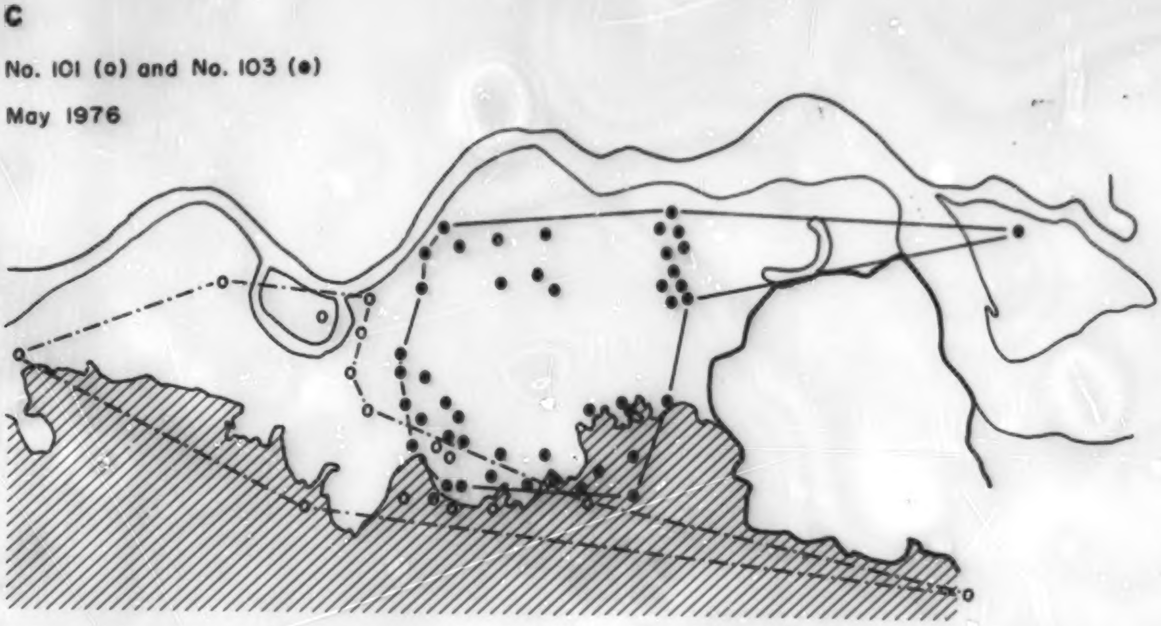

a
No. 101 (o) and No. 103 (●)
Mar 1976
Rapti River
N
Cultivation
0
1.6 km
Sal Forest
b
No. 101 (o) and No. 103 (●)
Apr 1976

FIGURE 25.—Areas used by female 103 and her mother (101): *a*, Mar 1976; *b*, Apr 1976; *c*, May 1976. (Circles = radio locations.)

of females 101, 106, and 107 did not overlap, nor did the ranges of two females at the western end of the park (McDougal, 1977). Another adult female (108) was captured in the northeast section of the park in April 1976, but since she died the same day her status is unknown. Number 108's presence was not detected in 1975, though baiting operations were conducted in 101's and 106's



range and in 1976, 108 was captured at a bait site near the eastern boundary of 106's range. Number 108 may have resided in the area between the ranges of 101 and 106 (Figure 27); this space has been occupied for at least two years by an adult female and her range does not overlap with those of neighboring females (J.L.D. Smith, pers. comm.). This pattern of exclusive ranges was also observed by McDougal (1977) at the western end of the park, although the situation there does not seem as stable as in the east. He has recorded some overlap in female ranges in space but not in the time of use.

Home range boundaries were, in some cases, demarcated by the Rapti River and the ridge of the Churia Hills, but there were no obvious discontinuities in the distribution of prey or habitat types on the floodplain which would account for the observed spatial distribution. Indeed, each female's range contained a similar extent of riverine forest and grassland. The river and ridge quite likely influenced the shape of home ranges, and facilitated the ease with which areas could be defended, but the topographic features do not explain the spacing pattern.

Tigers did not patrol their home range boundaries but most parts of their ranges were regularly visited, suggesting that exclusive rights to an area were maintained by other means. In addition, there was no evidence of overt defense of ranges by residents; none of the animals captured bore signs of having been in fights. Thus, it appears that the land tenure system is a form of territoriality maintained by the resident's presence, which can be advertised by conspicuous movements and various chemical and visual signs.

Discussion

Tigers in Chitawan are highly mobile animals, frequently changing locations from day to day, infrequently reusing rest sites, and often travelling considerable distances during a night of hunting. They were located in a different place on consecutive days about 72% of the time. By comparison, for leopards in Tsavo Park, Kenya, the figure was 87% (Hamilton, 1976) and for mountain lions,

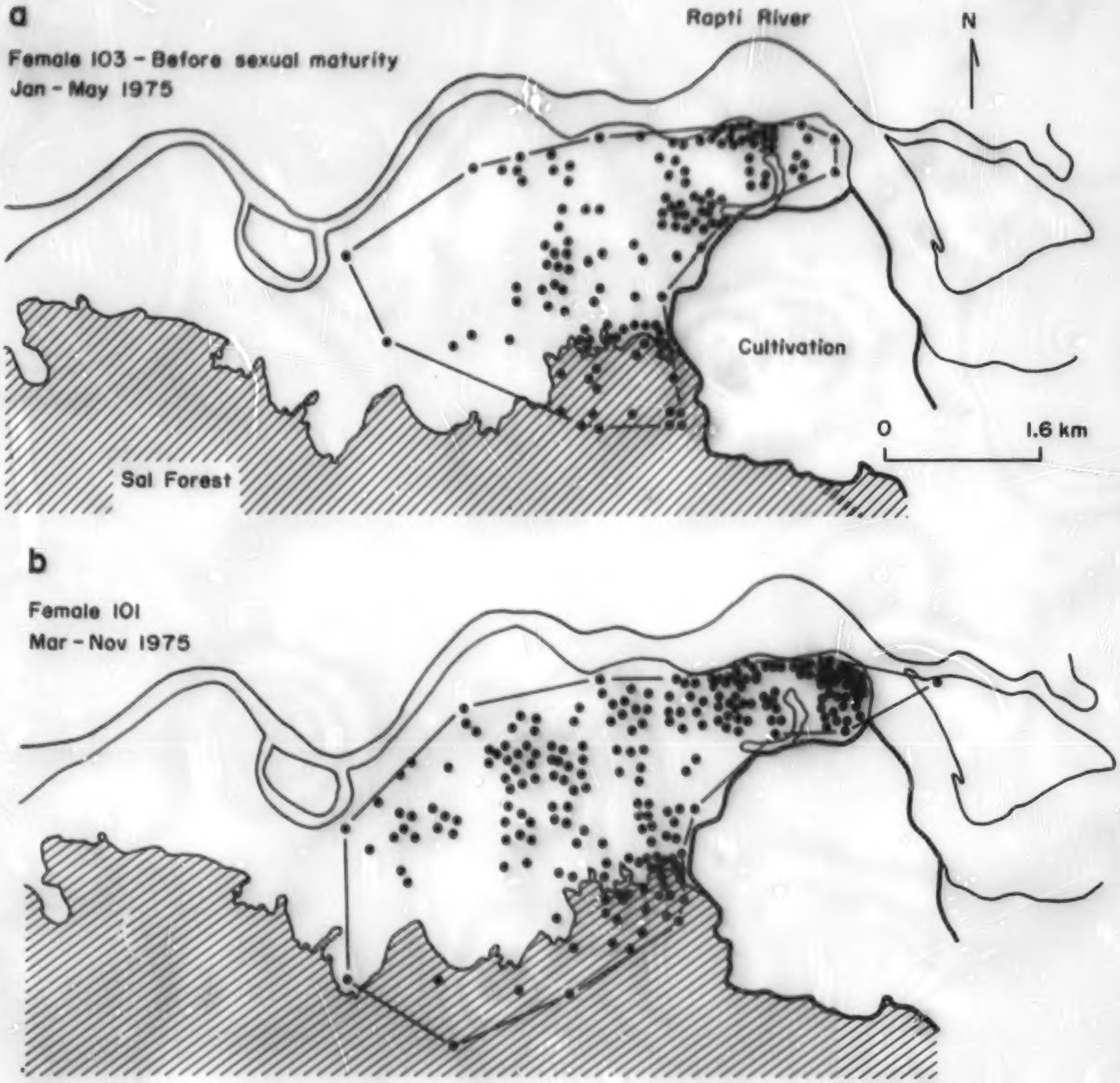
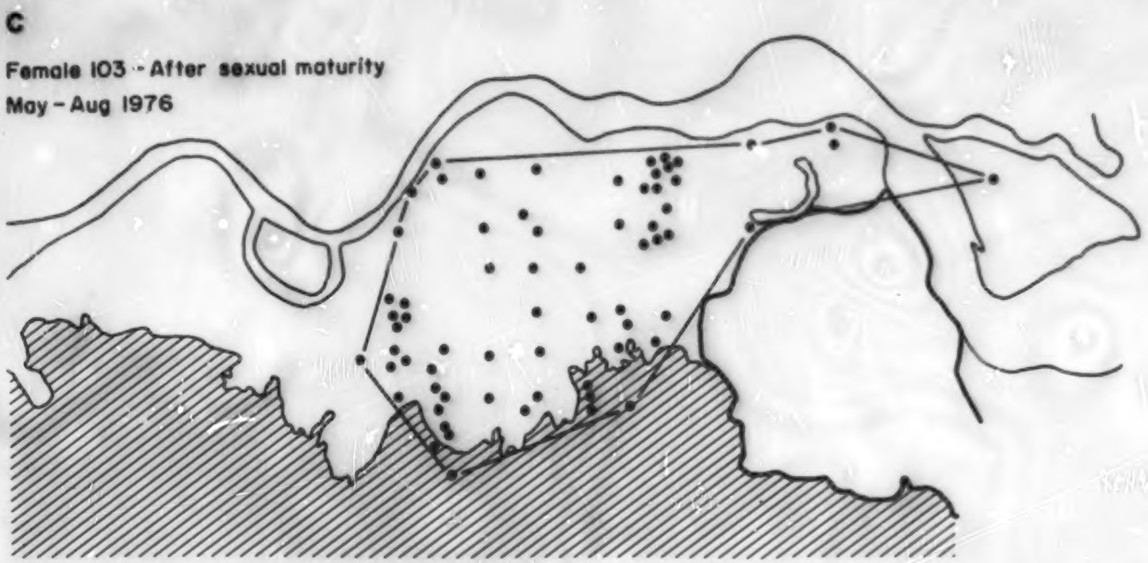

a
Female 103 - Before sexual maturity
Jan - May 1975
Rapti River
N
Cultivation
0
1.6 km
Sal Forest
b
Female 101
Mar - Nov 1975

FIGURE 26.—Areas used by females 101 and 103: *a*, area used by 103 as subadult; *b*, home range of mother; *c*, area used by 103 after acquiring her mother's home range (101 established new home range).

80% (Seidensticker, et al., 1973). Distances travelled in a night of hunting are extensive, I estimated 10–20 km/night for females in Chitawan and similar figures are available from other areas. Schaller (1967) estimated that tigers in Kanha Park, India, travel an average of 16–32 km during an unsuccessful night of hunting; in the Soviet Union tigers travel 15–20 km/day in the winter and rest six to eight times per 10 km (Matjushkin, et al., 1977). Daily movements of leopards in



Tsavo Park are similar to tigers in that they travel an estimated 10–25 km/day, with the majority of movement occurring at night (Hamilton, 1976).

The similar extensive movements and frequent changes in location exhibited by these big cats are obviously related in part to finding scattered prey in situations suitable for stalking, as departures from this pattern are often associated with kills (Seidensticker, et al., 1973; Hamilton, 1976; this study). They need to travel widely as they cannot continually exploit prey from one relatively small area and expect to be predictably successful (Charnov, et al., 1976); nor is it likely that a small area could totally support the energy requirements of a large predator (McNab, 1963). In addition, prey are likely to be active at varying times and changes in local conditions cause prey to alter their distribution patterns. In the short-term, an animal's home range is frequently changing as to when and where prey are to be found, but in the long-term conditions in some areas are more favorable for hunting. This was evident in Chitawan as a disproportionate number of kills (89%) were found in grassland and riverine forest ("Habitat Use"), where prey density and biomass are much higher (Seidensticker, 1976b; Tamang, 1979).

Not all of the tigers' extensive movements can be explained as hunting efforts; maintenance of exclusive ranges (territories) is also implicated as they regularly visit areas of low prey density (i.e., sal forest) where there is a low probability of hunting success. Only 11% of kills were found in these areas, although tigers were located in sal forest about 13%–30% of the time (Table 8); and visits to this habitat sometimes followed a period of feeding elsewhere and, as such, probably were not influenced by hunger. The inclusion of these less productive areas in an animal's home range space probably serves to ensure access to resources throughout the year and over several years, as each year local conditions change (grasslands flooded, cover for stalking reduced by burning), and, more importantly, resources are unlikely to remain stable in the long-term.

Movement data also showed that resident tigers regularly traverse their home range space, females commonly visited most parts of their ranges at intervals of a few days to two weeks, and the limited data on an adult male showed

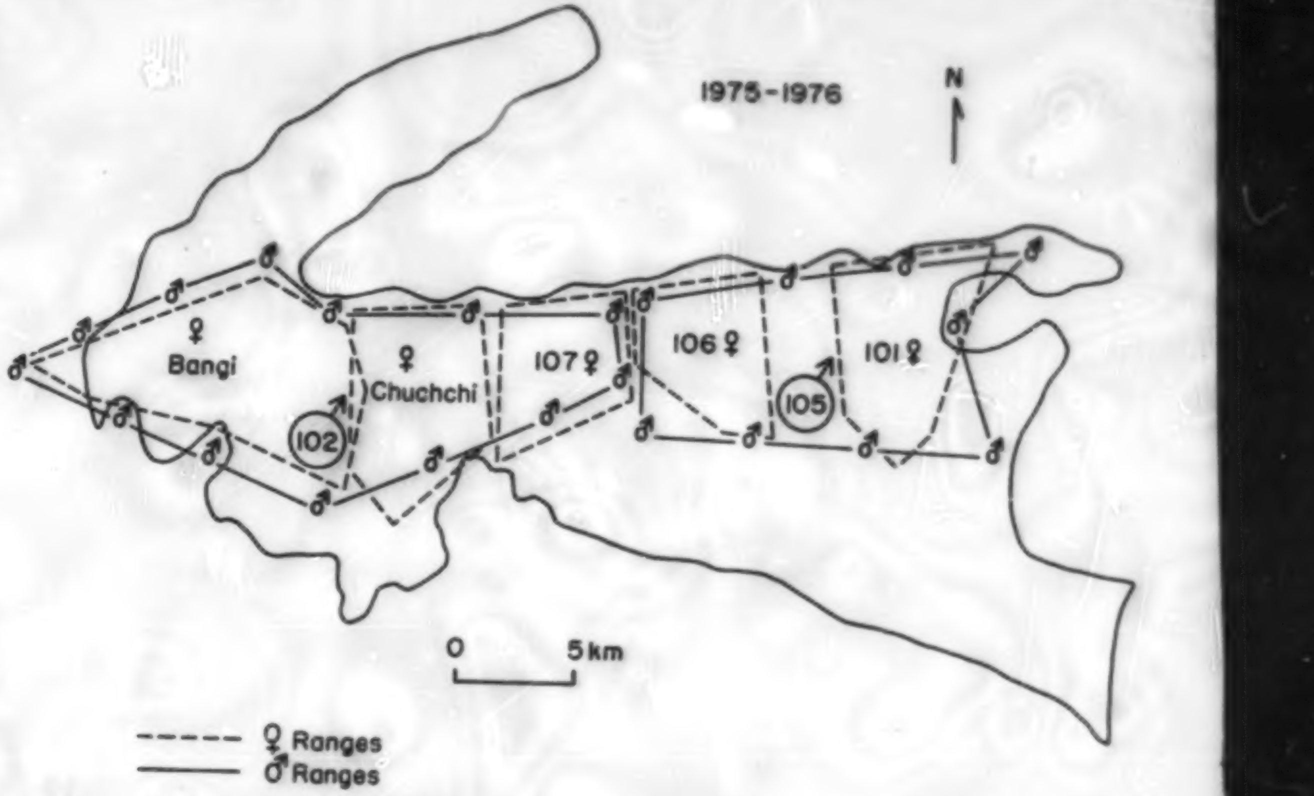


FIGURE 27.—Pattern of exclusive ranges of resident males 102 and 105 in relation to exclusive ranges of females 101, 106, 107, Bangi, and Chuchchi (location data on 107 from this study and Smith (1978); location data on 102 from this study and McDougal (1977), who also provided data on Bangi and Chuchchi).

the same pattern, with the longest interval between visits to one area being 15 days. McDougal (1977) also reported that tigresses regularly traverse their ranges, more often than males; and Schaller (1967) observed that some routes were used several times in one week by the same female, sometimes on consecutive nights. In Chitawan, and elsewhere, roads and trails play an important part in these movements, as the frequency with which tracks appear on the road indicates (Table 13). Many of the movements along roads were highly directional and tigers appear to be using these paths to facilitate quick and easy travel to other parts of their ranges, or to make short hops between hunting areas. Evidence of urine-spraying, conspicuous fecal piles, and associated scrapes were observed along the network of roads and trails (see "Communication"), and as these paths were commonly travelled by several tigers the potential for encounter and/or the exchange of various types of olfactory information is high (Montgomery, 1974). Given the relatively large ranges that tigers maintain, scent and visual marks would provide a convenient means to convey information (e.g., occupancy) to conspecifics (Eisenberg and Kleiman, 1972; Johnson, 1973). A similar situation is seen in brown hyaenas (*Hyaena brunnea*) (Mills, et al., 1980). Wolf packs (*Canis lupus*) visit most parts of their territories every three weeks or sooner, and scent marks are placed along territorial boundaries at a significantly higher rate than the interior (Peters and Mech, 1978). These researchers have shown that the stimulus value of scent drops to zero after approximately 23 days. This and similar evidence in the dwarf mongoose (*Helogale undulata rufula*) (Rasa, 1973) and golden hamster (*Mesocricetus auratus*) (Johnston and Lee, 1976) suggest that to be effective as indicators of occupancy scent marks have to be renewed or new marks laid down at intervals of three weeks or less.

The loss of two territories seen in this study was clearly associated with the cessation of visits by a resident animal to large portions of its range. In one instance an adult female (101) exhibited the typically restricted movements associated with the birth of young. In response to human disturbance she moved her litter to a far corner of her range and confined her activities to this area for a month. In 101's absence her sexually mature daughter (103) appropriated most of the unused portions of her mother's range, which she maintained exclusive rights to thereafter. During the time she was establishing her territority, 103 spent a disproportionate amount of time along those boundaries of her new range that abutted neighboring females (Figure 21). A similar pattern of movement has been seen in the Palm civet (*Nandinia binotata*), with individuals spending more time along the boundaries of newly established ranges (Charles-Dominique, 1978); and wolves significantly increase the frequency of scent-marking when they establish a new territory (Rothman and Mech, 1979). These observations suggest that during the initial period of establishing a territory, it is extremely important for an animal to intensively indicate occupancy.

Further support for the hypothesis that maintenance of exclusive rights to an area is involved in tiger movements are the observations of McDougal (1977), that even when animals are provided the basic requisites of food, cover, and water they do not localize their activities around bait sites but continue to travel extensively about their ranges. He also observed that when an occupant of a particular tract stops using it another tiger soon moves in; suggesting that in addition to visiting areas to possibly reinforce old scent-visual marks or to establish new marks, animals are evidently continually checking neighboring areas, making exploratory probes into them when a boundary or area has been unvisited (unmarked?) for some length of time. This behavior is also exemplified in the second example of home range acquisition, when a male (105) who had not been located in a neighboring male's (102) range in the preceeding 18 months, began using a portion of it within a month of 102's death (McDougal, 1977). Furthermore, having eventually doubled the size of his home range by appropriating part of 102's former range, male 105 continued to visit most parts of it at the same frequency (three to four times/month, J.L.D. Smith, 1978) with which he covered his previous smaller range (Table 12). In both these examples of range acquisition the time that elapsed between when an area stopped being used and when it was appropriated is remarkably similar, about one month, and coincides with the frequency with which tigers get to most parts of their ranges.

The extensive movements of tigers in Chitawan are clearly a strategy for locating and capturing prey, but there also appears to be pressure on residents to visit most parts of their exclusive ranges to ensure rights to the resources of an area. Their ranges are too large to be defined by physical presence alone (Leyhausen, 1965), and given the low visibility of the habitat and their nocturnal habits, the principal mechanism for establishing and maintaining exclusive use of an area is likely via the deposition of scent and visual marks along major travel routes and boundaries with neighboring animals (discussed in "Communication").

The land tenure system of solitary felids appears flexible and not surprising home range sizes vary considerably (Table 16). On the flood plain at Chitawan, both male and female tigers maintain mutually exclusive ranges; the larger male ranges (60–100 km^2) overlapping three to six smaller female ranges (16–20 km^2). McDougal

TABLE 16.—Home range, habitat type, prey characteristics, and land tenure system of some felids (E = exclusive range; 0 = overlapping range; E/O = seasonally variable; * = minimum range)

Species	*Home range size (km²)*		*Habitat classification*	*Prey characteristics*	*Land tenure system*		*Location*	*Source*
	M	*F*			*M*	*F*		
Tiger	60-72*	16-20*	Moist, semideciduous forest/gallery forest with alluvial plain	Abundant, widely distributed, small-large size, stable	E	E	Chitawan	This study
	90-105	26-39	Moist, semideciduous forest/gallery forest with alluvial plain	Abundant, widely distributed, small-large size, stable	E	E	Chitawan	McDougal (1977)
	78	65	Moist, semideciduous forest with meadows	Abundant, smal-large size, seasonal concentrations	E	O	Kanha	Schaller (1967)
	30-50*	10-20*	Moist, semideciduous forest, with meadows	Abundant, small-large size, widely distributed, and increasing	E	E	Kanha	Panwar (1979)
	38-50*	12-42*	Moist, semideciduous forest	Abundant, small-large size, seasonal concentrations	O	O	Palamau	Sinha (1979a)
	800-1000	100-400	Mixed coniferous and hardwood forest	Uneven distribution, small-large size, large seasonal movements	E	O	USSR	Matjushkin, et al. (1977)
Mountain lion	453*	170-375*	Montane forest	Abundant, small-large size, seasonal movements	E	O	Idaho	Seidensticker, et al. (1973)
Jaguar	50-76*	25-38*	Moist, semi-decid forest/gallery forest and alluvial plain	Abundant, small-large size	E	O	Brazil	Schaller and Crawshaw, 1980
Leopard	9-10*	8-10*	Dry, semi-decid forest and evergreen scrub	Abundant, small-large size, concentrated around large villus	E	E	Sri Lanka	Eisenberg and Lockhart (1972)
		40-60*	Wooded grasslands	Abundant, small-	E	O	Serengeti	Schaller (1972)
	9-63*	29*	Dry, grassland, montane forest and bushland	Common to abundant, small-large size	E	O	Tsavo	Hamilton (1976)
	10-19	10-19	Dry, open woodland and grassland	Abundant, small-large size	E	O	Rhodesia	Smith, R.M. (1978)
Bobcat	2-4*	3-5*	Deciduous, bottomland, swamp	Abundant, small size	E	E	S. Carolina	Provost, et al. (1973)
	6-108*	9-45*	Sagebrush-grass	Abundant, small size, localized	E	E	Idaho	Bailey (1974)

TABLE 16.—continued

Species	Home range size (km²)		Habitat classification	Prey characteristics	Land tenure system		Location	Source
	M	F			M	F		
Lynx	14–25*	10–26*	Boreal forest	Abundant, small size, localized, increasing after "crash"	O	E	Alaska	Berrie (1973)
	18–21*	16*	Boreal forest	Small size	E	E	Newfoundland	Saunders (1963)
Lion	–	25–114	Woodlands	Abundant, small-large size, non-migratory	–	E	Seronera	Bertram (1978)
	–	30–400	Woodlands/plains	Small-large size, seasonally abundant	–	E/O	Serengeti	Schaller (1972)
	–	19–31	Tropical savanna	Abundant, small-large size, some migratory	–	E/O	Nairobi	Rudnai (1973)
	–	119–275	Semi-desert	Most small, widely distributed	–	O	Kalahari	Eloff (1973a)
Cheetah	102	76–82	Tropical savanna	Abundant, small-large size, some migratory	–	O	Nairobi	McLaughlin (1970)
	–	51–130	Tropical savanna	Abundant, small-large size, some migratory	–	O	Nairobi	Eaton (1974)
	–	60–65	Woodlands/plains	Small-large size, some migratory	–	O	Serengeti	Schaller (1972)
	12–36	800	Short-medium grasslands	Small-large, seasonally abundant	E	O	Serengeti	Frame (1980)

(1977) reported female ranges in Chitawan of 26–39 km², but when computed by the "minimum area method" range sizes are similar to those recorded for females in this study (McDougal, pers. comm.). Mutually exclusive to completely overlapping female tiger ranges, and overlapping and mutually exclusive male ranges, which encompass those of females, have been reported for Palamau Reserve and Kanha Park, both in north-central India (Sinha, 1979a; Schaller, 1967; Panwar, 1979). In the Soviet Union female ranges, measuring 100–400 km², overlap partially, while males occupy exclusive ranges up to 800–1000 km², which overlap those of females (Matjushkin, et al., 1977).

Seidensticker, et al. (1973) found the large ranges of female mountain lions (170–375 km²) to overlap partially to almost completely in some cases, while the larger male ranges (453 km²) showed little overlap except with those of females. A similar pattern has been observed in the jaguar (Schaller and Crawshaw, 1980). In Sri Lanka, male and female leopards share small (8–10 km²) mutually exclusive ranges (Eisenberg and Lockhart, 1972; Muckenhirn and Eisenberg, 1973); whereas in the Serengeti, Tsavo, and Rhodesia, female leopard ranges overlap somewhat and those of males are exclusive but overlap several females (Schaller, 1972; Hamilton, 1976; R. M. Smith, 1978). In the smaller bobcat and lynx, females tend to occupy exclusive ranges, and while male ranges encompass those of females, their ranges may or may not be mutually exclusive (Provost, et al., 1973; Bailey, 1974; Saunders, 1963; Berrie, 1973).

Throughout their wide geographic distribution, solitary felids encounter a variety of habitat types and corresponding variations in resource availability and dispersion. Consequently their land tenure systems exhibit a great deal of flexibility, inter- and intra-specifically. The most commonly observed pattern is one in which males occupy large, exclusive ranges within which are several overlapping female ranges. However, where variations occur, it is most evident in female ranges. Several females may share one large range, but have separate core areas or use a common space at different times; their ranges may overlap partially; or as was found in this study, females occupied small exclusive areas.

Overlapping male ranges have been reported on a few occasions (Table 16), but these may be explained as a male temporarily residing within a resident's range (e.g., 104 in 105's area), or that in marginal habitat adjoining core areas young adult males may share areas prior to establishing an exclusive range of their own. This variability clearly indicates that the status and relationships of individuals, and the environmental setting, need to be known to begin to interpret the flexibility in social systems.

The flexibility seen in the social systems of solitary felids is also evident in many other carnivores, (Kleiman and Eisenberg, 1973; Herrero, 1978; Bekoff, 1978; Fox, 1975; Macdonald, 1979; Kruuk, 1975). In general correlates can be drawn between the social system and various ecological factors such as habitat structure, prey size, distribution and density. These factors influence the social interactions and movement patterns of individuals and hence shape the overall social organization of the population.

The major factor influencing this variability is most certainly the seasonal distribution and abundance of prey. In a situation where prey are widely distributed and/or make extensive seasonal movements it should be adaptive for a predator to use a large range. Such extensive ranges would also be likely to overlap with conspecifics as the cost of maintaining exclusive rights to such a large area becomes uneconomical (Brown, 1964). This probably explains the overlapping ranges of tigresses in the Soviet Union where prey are migratory in response to climatic changes (Matjushkin, et al., 1977). A similar situation is apparent in the ranges of female mountain lions reported by Seidensticker, et al. (1973). The exclusive ranges of males under these conditions suggests that the benefits of exclusivity are greater for males than for females.

The maintenance of relatively small, mutually exclusive ranges in Chitawan appears to be favored primarily by a seasonally stable prey population that is more or less evenly distributed throughout the floodplain environment. Data from radio-tracking shows that sambar, chital, and hog deer, the major prey species, confine their movements to small areas (0.5–10 km^2, Tamang, pers. comm.) where they are apparently able to satisfy their resource requirements on an annual basis. In addition, prey density and biomass are high (Seidensticker, 1976b; Tamang, 1979), a characteristic feature of alluvial plain habitats (Eisenberg and Seidensticker, 1976).

A similar situation is evident in Sri Lanka, where leopards living around large, scattered lakes ("villus") maintain small, mutually exclusive ranges (Eisenberg and Lockhart, 1972; Muckenhirn and Eisenberg, 1973); a spatial distribution they have shown to be related to an abundant but localized prey base. The exclusive female ranges of bobcat and lynx have also been related to the localized distribution of prey and topographic features (Bailey, 1974; Berrie, 1973).

Somewhat intermediate in terms of social structure is the situation in Kanha Park, India, where in 1964–1965 Schaller (1967) reported female ranges overlapped almost completely, with as many as three females using the same area. A male tiger in the same area did not share his range with other males but his range overlapped those of the females. Interestingly, the social system in Kanha may have been altered in response to changing environmental conditions. The area was declared a tiger reserve in the early 1970s and a concerted effort was made to improve habitat quality by removing 25,000 head of cattle, providing permanent water sources, and controlling annual burning. These efforts were successful, and there has been a dramatic increase in the numbers of grazing species (Coe, 1979). Panwar (1979) reports that in the same area females are now utilizing smaller, non-overlapping home ranges, suggesting that in Kanha we may be seeing a flexible social system in operation.

While dispersion and availability of prey and other habitat characteristics are important determinates of range size and the degree to which resources can be monopolized, the distribution of conspecifics must also be considered. Sexual differences in the size of home ranges of many mammals have been explained to a large extent by differences in body weight (Harestad and Bunnell, 1979) but, using their criteria, tigresses should have ranges 39%–47% the size of males. On the floodplain in Chitawan this is not the case. Female ranges were between 16%–33% (16–20 km^2 versus 60–100 km^2) of a male's. I suggest that this is strongly influenced by the fact that about 50% of the male's range bordered on agricultural land, and as such, was not subject to encroachment by other males. Additional factors influencing the size and energy required for defense of this male's range may have been the park road, which facilitated travel through the area (J.L.D. Smith, 1978), and the occasional provisioning of baits. Without these influences this male would probably not be able to maintain exclusive rights to such a large area and the females contained therein.

The agricultural land bordering the park probably also influences the size of female ranges, and these too may be larger than necessary. In terms of a "defendability index" (Mitani and Rodman, 1979), where a value of 1.0 indicates the possibility of crossing the diameter of a circular range once a day, tigresses in Chitawan have a low index value, about 0.3 to 0.6. According to their calculations for primates, territorial species have high index values (>1.0). Tigers are highly mobile, a feature also characteristic of territorial primates (Mitani and Rodman, 1979), but to achieve an index value greater than 1.0 tigresses would have to travel on the average about 30 km per day, rather more than the 10–20 km/day estimated in this study. However, agricultural land bordering their ranges would reduce the time and energy required for maintenance. Furthermore, tigers would not need to travel as far as suggested above if scent marks function as proposed, and the observations indicate that while tigers can and occasionally do cross their ranges in a single night, most parts are visited at much less frequent intervals.

A further influence on social structure, but one not encountered in this study, may be the presence of a competitor. The Indian wild dog (*Cuon alpinus*) has been known to drive tigers off kills, and even to kill them (Schaller, 1967:235). The extent to which the two species compete for resources is not known, but observations from one area (Johnsingh, 1980) indicate a large degree of overlap not only in the use of space, but also in the size of prey taken. The distribution and number of competing predators is likely to affect the socio-spatial organization of tigers, resulting in generally larger, overlapping female home ranges.

It can also be seen that the pattern of ranges exhibited by tigers would, in effect, limit the number of residents that could be contained within a given area. What is happening with animals that do not obtain territories within the core area (prime habitat) is currently under study; but it is evident from the observed social organization in Chitawan that the sex ratio in core areas favors females (1 : 4) over males. The sex ratio at birth is parity (Schaller, 1967; Sankhala, 1967) and the differences cannot be totally accounted for by mortality of males. Preliminary results from Kanha Park (Panwar, 1979) suggest that a different social system is operating outside core areas; with a preponderance of males being found in these less productive habitats, and the little available evidence suggests that breeding success is low in this segment of the population. Competition for breeding sites is high, as evidenced by the speed with which vacant sites are occupied, and while I found no evidence of fighting, J.L.D. Smith (1978) has recorded several fights involving some of the same individuals that I monitored. A situation where there is a high production of young within small isolated reserves lacking suitable neighboring marginal habitat, could result in increased damaging intraspecific conflicts, and eventual conflict with man and his livestock.

Social Interaction Patterns and Communication

METHODS

An estimate of the degree to which tigers socialize was examined by calculating the linear distance between animals located on the same day. The individuals involved included an adult male, 105, and three adult females, 101, 103, and 106, all of which resided within the male's range. Two independent offspring, male 104 and female 103, of female 101 also used part of the male's range; female 103 was radio-tracked as both a subadult and as an adult. The extent of overlap in the movements of these tigers is shown in the section on "Home Ranges." The figures represent minimum estimates of social contact since continuous monitoring of their movements was not feasible and animals were not usually located more than once a day. The overall time difference between locations averaged 90 minutes (range 1–600 minutes, N=834), but if two tigers were close together this difference was minimal (<5 minutes). To determine if animals were actually together, additional bearings were obtained while circling the pair at close range (100 m).

Data on communication were limited to indirect and long-distance circumstances involving olfactory, visual, and auditory signals.

SOCIAL INTERACTIONS

In the following sex and age comparisons, the distribution of distances between individuals indicates that even tigers with a large degree of home range overlap are not often found together, but are more commonly two to five km from each other.

ADULT MALE–ADULT FEMALE.—Radio-location data for adult male 105, and adult female 101 were obtained from 3 March to 15 August 1975, and again from 31 December 1975 to 21 May 1976. A frequency distribution of the distances between their locations is shown in Figure 28. On 75% of the days when both animals were located (78 of 104), they were separated by at least 1.6 km, and the mean distance (km ±s.e.) was 3.7 ±0.3 km (N=104). On 14 occasions less than 0.8 km separated their locations, on one they shared a natural kill, and twice they rested along the same stream, but not together, the remaining 11 occasions were related to suspected heat periods. On only seven of the 14 occasions were they actually together, the longest period of which was two days.

The following observations on 105 and 101 are examples of the way movement and behavioral changes were associated with suspected heat periods.

In the month preceding the birth of her young, female 101 was not found within 400 m of the adult male, though they were both located almost daily during this period. On 15 April 1975, 101 lost her 11-day-old cubs in a grass fire; 17 days later, on 1 and 2 May, she was in close association with the adult male, indicating that she was probably in heat. They were together again on 7 May, after which they were not associated until 27–28 May, presumably the latter date marked a second heat period.

During the daylight hours of 1 May the pair were located together in a tall-grass area near a stream. Pugmark data indicated that later that night the male followed the female down the park road for 0.8 km before they turned off onto a trail. They were located together again the next

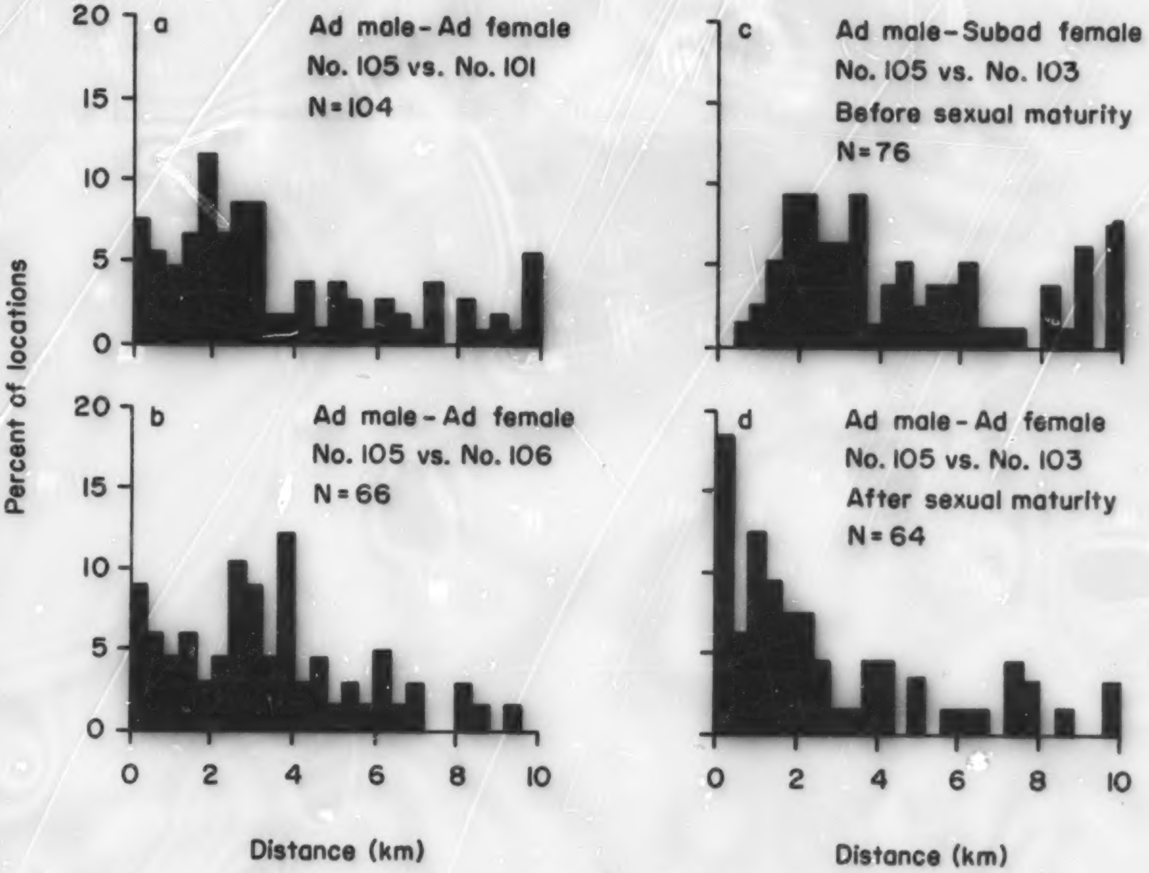


FIGURE 28.—Frequency distributions of distances between adult male 105 and adult female 101 (*a*) and 106(*b*); distances between 105 and female 103 before (*c*) and after (*d*) she reached sexual maturity. (N = approximate number of days on which both animals were located.)

morning, on 2 May, 1.6 km from the previous day's rest site, in another tall-grass area. On 3 May, 101 was observed with her daughter, 103, on the park road, and male 105 was located 8.0 km away, the pair having obviously split. The pair were together again on the 7th of May, in the same tall-grass area they were found in on the 2nd of May. From 0800 to 0945 hrs both animals were inactive (based on radio-signals), but at 1000 hrs the female suddenly left, and 30 minutes later she was located two km away while the male remained in the area. No vocalizations were heard, though I was in a tree about 50 m away from the pair. The following morning the male, 105, was located about five km from the female, 101, well out of her home range.

The pair was not found together again until 27–28 May, and in the interim 101's behavior suggested that she was not in heat. Kleiman (1974) reports that urine spraying is a common behavior after and between heat periods, and on 11 May I followed 101's tracks (distinguishable by an unusual pattern) down the park road for 3.2 km, she had scent-marked 17 trees and one bush over this distance. She had marked objects along this same path during the previous two months, but certainly not at this frequency, where in some sections her tracks indicated she had detoured from the road every 50–75 m to mark trees.

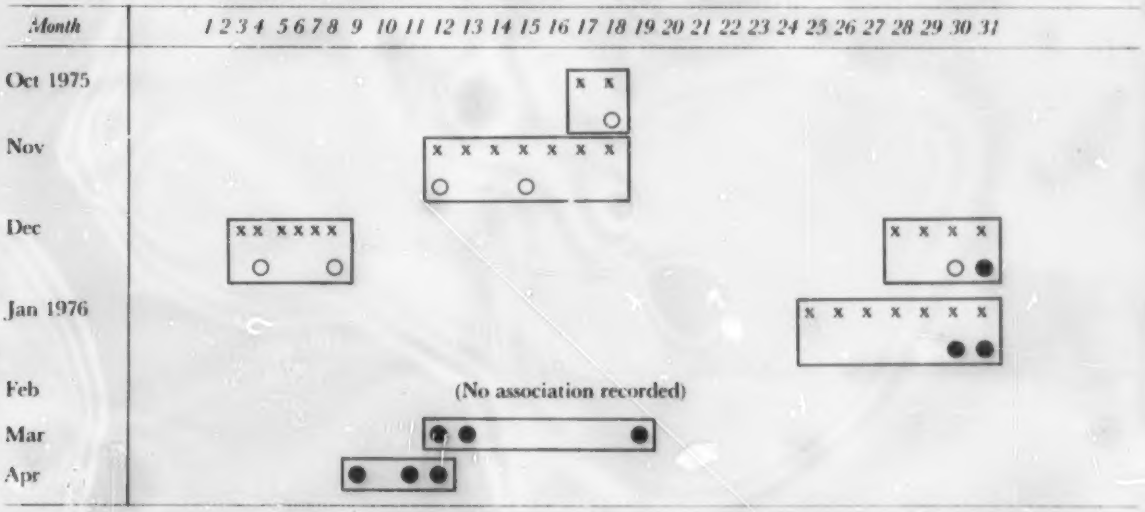
Female 101 gave birth to a new litter on about 14 December 1975, which means conception occurred about 1 September, and between 31 December 1975 and 8 March 1976 the pair was not found within 0.8 km of each other. They were together on 9 March, and again on 27 March which presumably meant that 101 had lost her litter, as females with small cubs do not usually associate with males (see "Discussion"). She was observed in May 1976 without young, and in December 1976 she produced another litter (Smith and Tamang, 1977).

Radio-location data for male 105 and another adult female, 106, were obtained from 16 February 1975 to 15 August 1975, and again from 2 February 1976 to 26 June 1976. A frequency distribution of the distances between their locations is shown in Figure 28. On 75% of the days when both animals were located (49 of 66), they were separated by at least 1.6 km, and the mean distance (km ±s.e.) was 3.4 ±0.3 (N=66). They were within 0.4 km of each other on six occasions but they were not together. On two occasions, both at kills, they were about 100 m from each other. No association lasted for more than one day.

Adult Male–Female before and after Reaching Sexual Maturity.—Location data on subadult female 103 and male 105 were obtained between 23 January 1975 and 15 August 1975. During this period 103 was an estimated 20 to 28 months old and had not reached sexual maturity. A frequency distribution of the distances between their locations is shown in Figure 28. It was not known if 103 avoided 105, or vice versa, but at no time were the two animals found within 0.4 km of each other, and on only one occasion were they located within 0.8 km of each other. During this period over 90% of their locations were separated by more than 1.6 km, and the mean distance (km ±s.e.) was 5.0 ±0.4 km (N=76).

With the apparent onset of sexual maturity in 103 her behavior changed and an adult male began showing an interest in her. She was an estimated 30 months old when she appeared to have her first heat period. She began roaring in October 1975, and over the next several months she was heard to roar at regular intervals (Table

Table 17.—Dates of suspected heat periods of female 103 as indicated by roaring and visits by adult male (x = roaring by female; ○ = visits by adult male, probably 105; ● = visits by 105; boxed dates = suspected heat periods)



Month	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Oct 1975																	x	x ○													
Nov												x ○	x	x	x ○	x	x	x													
Dec			x	x ○	x	x	x	x ○																				x	x	x ○	x ●
Jan 1976																									x	x	x	x	x	x ●	x ●
Feb	(No association recorded)																														
Mar												●	●						●												
Apr									●		●	●																			

17). Roaring was heard in what appeared to be other situations, but in the case of this tigress it was conspicuous by its regularity and frequency. The call was also resonant, as I clearly heard it from as far away as 3.2 km. During five suspected heat periods she initially roared only at night, but after two to three days, she was also heard roaring during the daytime. At the same time, the frequency of roaring increased from two to three times/night to 10–12 times/day. On two different occasions this tigress roared 69 times in 15 minutes. While an adult male visited her (based on tracks) during each of her suspected heat periods in October, November, and early December, 1975, the presence of the resident male (105) was not confirmed until he was captured in her area on 31 December 1975; he had lost his radio-collar. However, since no other adult male was ever located in this area, the male in question most likely was 105. Data presented in Figure 28 are from locations obtained between 1 January 1976 and 30 May 1976. During this period only about 53% of their locations were separated by more than 1.6 km and the mean distance (km ±s.e.) was 2.8 ±0.4 km (N=64). This is markedly different from the previous observations. On 16 occasions less than 0.8 km separated their locations, and every instance was associated with suspected heat periods. Of 12 locations when the pair was separated by less than 0.4 km, they were probably together on five, and for the remainder, they were judged to have been within 100 m of each other. During one heat period the pair crossed a broad floodplain at the same time, in places their tracks were found to be 40–50 m apart and at other points the male was apparently following the female. The pair was, however, never found together for more than two consecutive days.

ADULT FEMALE-INDEPENDENT OFFSPRING.—In young tigers the transition from total dependence on their mother to complete independence is characterized, at least in part, by a gradual decrease in the frequency of association between mother and young (Schaller, 1967; McDougal, 1977). The extent to which independent young (predispersal) continue to associate with their mother was examined using radio-location data on two independent siblings (103, 104) and their mother (101). During this period (3 March 1975 to 24 October 1975) the siblings were an estimated 22 to 30 months of age. Frequency distributions of the distances between the locations of the tigress and her offspring are shown in Figure 29.

The home ranges of the tigress (101) and her daughter (103) were relatively small and overlapped almost completely, thus the distances between their locations are not large. On 55 of 118 locations (47%) they were within 1.6 km of each other, and the mean distance (km ±s.e.) was 2.2 ±0.2 km (N=118). However, on only four occasions where they actually found together. On the day 101 was thought to have given birth to a new litter, she and 103 were together in the area where the young were born. On another occasion they were located about 2.0 km from each other in the morning, but they were together that night, where from one small area several bouts of roaring and snarling were heard over a two-hr period. The following morning a partially eaten yearling male sambar was found about 150 m from where the females were located the night before; both tigresses were nearby but about 400 m apart. There was no drag mark, indicating that the animal was killed where it was found, and judging from tracks, two females had been at the carcass. At their earlier location the grass over some 40 m^2 was flattened, and a small amount of deer hair was present; no blood or tiger hair was found. It was surmised that the females had cornered an animal but were not successful in killing it, at least not at that location. This was the only suggested incidence of cooperative hunting recorded during the study.

The subadult male (104) and his mother (101) were not found together during eight months of observation; although on 39 of 112 locations (35%) they were within 1.6 km of each other and the mean distance (km ±s.e.) was 2.5 ±0.2 km (N=112). In one instance, when 104 was with a large kill, his mother was located within 100–200 m of him. One night they were in the same

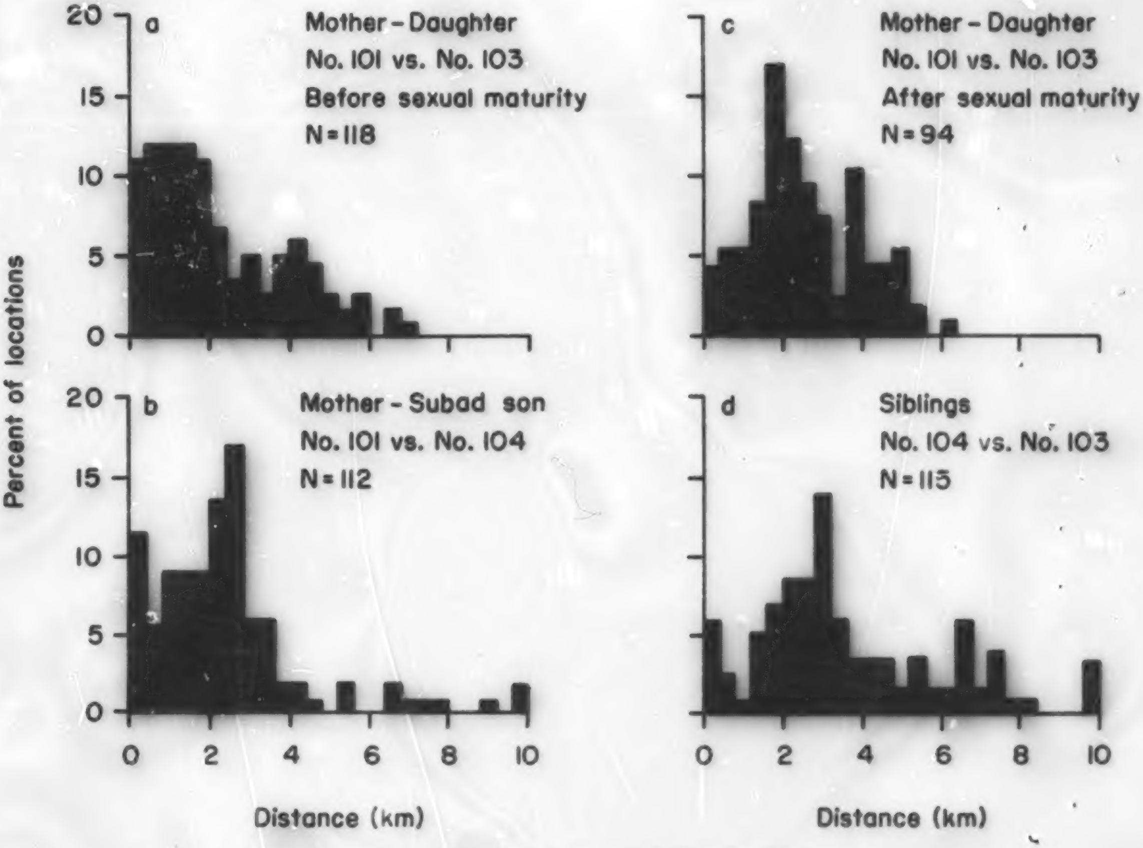


FIGURE 29.—Frequency distribution of distances between pairs: *a*, adult female 101 and her independent offspring 103; *b*, 101 and her independent offspring 104; *c*, 101 and sexually mature 103; and *d*, siblings 104 and 103. (N = approximate number of days on which both animals were located.)

general area for about two hours, but each was in a different area when relocated several hours later. The subadult male, unlike the resident male, was not located with 101 when she was in heat, suggesting that he was not sexually mature. He was, however, located within 200–300 m of the pair (101 and 105) during two suspected heat periods.

INDEPENDENT SIBLINGS.—Radio-location data for the two independent siblings (103, 104) were obtained from 23 January 1975 to 24 October 1975; during which time they were estimated to be 20 to 30 months old. Despite their sibling status, they were not commonly found close together (Figure 29); on 98 of 115 locations (85%) they were located at least 1.6 km from each other and the mean distance (km ±s.e.) was 3.9 ±0.3 km (N=115). They were located together on five instances in the period from 23 January to 27 February 1975, but on only two occasions in the following nine months were they located within 0.4 km of each other. Their longest period of association was two days. Two of their associations were at kills, a natural and a bait kill. They were disturbed at the site of the natural kill and even though they left the area in different directions and at different times they were together again when relocated six hours later, about 1.6

km from the earlier location. On another occasion they were together when located at 0820 hrs, but when relocated two hours later, the male had moved off about 0.5 km.

ADULT FEMALES.—The presumptive home range boundaries of females 101 and 106 were separated by about 3.2 km, and in the 17 months preceding 106's death she had not been located in 101's range. On only one occasion during this same period was 101 located in 106's range, and this occurred shortly after 101's range was taken over by 103 (see "Home Ranges").

As previously noted, 103 began showing signs of coming into heat in October 1975, and from then until August 1976 the distances between her and 101 were used as an adult female comparison. During this period 103 acquired 101's area, and 101 established a new range in an adjacent area. On only nine occasions (10% of locations) were 101 and 103 located within 0.8 km of each other (Figure 29), and almost all of these locations were along the periphery of their ranges. At no time were the females found together, but one night both were located in the same area along a presumed territorial boundary within 15 minutes of each other. The mean distance (km ±s.e.) between their locations was 2.6 ±0.1 km (N=94).

ADULT MALE–SUBADULT MALE.—Location data for a subadult male (104) and the resident male (105) were obtained between 31 December 1974 and 15 August 1975. During this period 104 was estimated to be 19 to 28 months old and he ranged over the same area as did 105. The distribution of distances between their locations (Figure 30) suggests that they associate more frequently than other tigers, but 65% (26 of 40 locations) of the closer distances (<1.2 km) are related to joint use of a specific rest area. On 14 occasions in April and 12 in May (1975) the two males were located along the same stream, the distances between them varying from 0.2 km to 1.2 km. Their longest period of association at this site was on four consecutive days; they would leave the area in late afternoon or early evening and return to it in the morning, but the direction and time of departures and arrivals did not suggest that they travelled together. Maximum daytime temperatures averaged about 37°C in April and May, and the attractiveness of this area was apparently the permanent stream and shade provided by tall, dense grasses. The subadult male rested in this area on 30 days in April-May and the adult male on 20 days in the same period. No aggression was recorded between the males at the rest area, though on one occasion a female (101) in heat was nearby. At no time were 104 and 105 judged to have been actually together, although on two occasions, both at bait kills, they were within 100 m of each other. The mean distance (km ±s.e.) between their locations was 2.6 ±0.3 km (N=85).

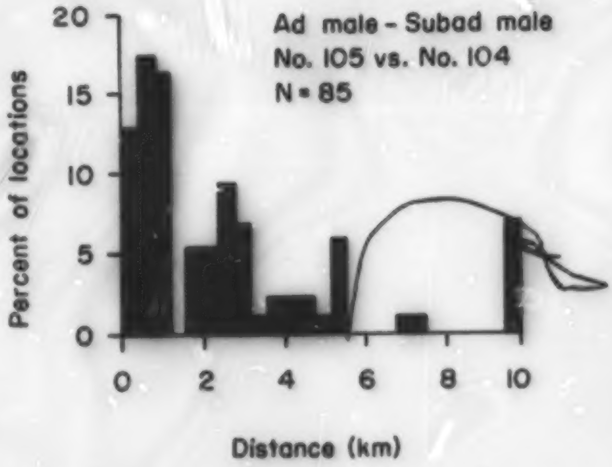


FIGURE 30.—Frequency distribution of distances between adult male 105 and subadult male 104 (N = approximate number of days on which both animals were located).

Another estimate of the degree to which tigers socialize was determined by an association frequency, defined here as the number of locations on which tigers were found within 0.4 km of another tagged tiger. As shown in Table 18, association frequencies ranged from 6% to 18%. The values for the males (104, 105) are higher because of their associations at a rest site, and the adult male (105) was associating with two adult females (101, 103). Overall, adult and independent subadult tigers appear to socialize infrequently with other tigers.

TABLE 18.—Frequency of association of adult and independent subadult tigers in Chitawan Park

Tiger no.	Age/sex	No. of radio-locations	Locations within 0.4 km of another radio-tagged tiger	
			N	*%*
101	adult F	391	38	10
102	adult M	16	1	6
103	subadult F	198	20	10
103	adult F	245	16	6
104	subadult M	218	33	15
105	adult M	203	37	18
106	adult F	135	8	6
107	adult F	16	1	6

A breakdown of the number of occasions when animals were within 0.4 km of each other, by sex and age combinations, shows tigers in close association in the following descending order of occurrence:

Adult male/Adult female	27
Adult female/Subadult male	15
Adult female/Subadult female	13
Adult male/Subadult male	11
Subadult male/Subadult female	7
Adult female/Adult female	4
Adult male/Subadult female	0
Adult male/Adult male	0

It should be noted, however, that while tigers were occasionally found within 0.4 km of another tiger, they were not often actually located together. Adults of the opposite sex were close together primarily for mating, and while tigers do socialize at bait kills, few associations were recorded at natural kills. Only five of 38 (13%) natural kills were shared and on only two of these occasions were two adults present. At 56 bait kills, however, at least 19 (34%) were shared, and the animals involved usually included a female and young or subadults, although an adult male was also present on a few occasions. Excluding the mating and kill situations, tigers were close together at rest sites and at other times they were probably hunting in or moving through the same area. Their associations were apparently brief, however, lasting for only a few hours to about half a day in the case of rest sites.

SCENT AND VISUAL MARKING

Scent-spraying, as described by Schaller (1967: 252), was not observed in this study although evidence of this behavior was detected on many trees and shrubs along the side of roads and trails. One tree situated at the intersection of three travel routes was scent marked by an adult male (based on tracks) at least three different times, but it was not near the boundary of any known territory. Urination without spraying was also noted; on two occasions a tigress appeared to have simply stopped, urinated, and then continued along the road.

Feces and scrapes (vegetation and substratum scraped clean by action of tiger's hind feet) are also reported to have communicatory functions (Schaller, 1967). A total of 55 tiger feces was collected in Chitawan during the cool and hot seasons of 1975 and 1976. Two fecal piles were found near kills, three were in grass areas, and the remainder (91%) were discovered at the side of or in the center of roads and trails. Tracking efforts were confined almost exclusively to roads and trails, thus the probability of finding feces was biased toward these sites. No feces could be positively attributed to a specific individual, but presumably most were deposited by residents. Feces were not covered and only four of 55 feces (7%) were associated with a scrape. At two scrape sites the amount of fecal material was much smaller than that of a normal scat and probably corresponds to what Schaller (1967) described as a "token" amount. Most fecal sites were not reused, although six feces were found at one site in a 3-month period. At another site two fecal piles, with scrapes, were found on 11 and 14 February, 1976, and tracks of an adult male were present on both occasions. This location coincided with the presumed eastern boundary of male 102's range, who was located at this site on 13 February, 1976, suggesting that males mark their territorial boundaries.

Eleven scrapes were found in the grass along the sides of roads and trails. They measured 30–50 cm long, 15–25 cm wide, and one to three cm deep. Both males and females made scrapes, as evidenced by tracks. Most scrape sites did not appear to have been reused although these sites were not regularly checked. A pungent odor was detected at eight of the 11 sites and on four occasions was associated with feces, indicating that scraping and scent-marking sometimes occur together. Both feces and scrapes were found in places that could be considered conspicuous in the sense that they were along frequently travelled routes and at intersections of roads and trails.

Tigers are also reported to use scratching trees as part of their communication repertoire (Schaller, 1967), but this was not observed to be an important mode of communication in the northeast part of the park. Claw marks of tiger or leopard were found on a log crossing a stream, but no trees with scratches were noted, although at the western end McDougal (1977) has reported seeing trees that showed signs of recurrent scratching by tigers.

VOCALIZATIONS

Roaring and moaning, which are placed in one category since they represent variations of the same basic vocalization (Schaller, 1967), were heard on only 92 occasions during the study. In most instances, calling consisted of one to six successive moans or roars by one animal, although a tigress in heat roared 69 times in 15 minutes. Fifty-six instances of calling were recorded at night, and at least 51 instances (55%) were associated with suspected sexual activity; all of the latter were related to tigress 103. More vocalizations were heard in the cool and early part of the hot season (November to April) than at other times of the year; although it should be noted that while time in the field was about equal from October to June, it was markedly reduced by climatic conditions from June through September. The number of times these calls were heard in Chitawan is shown below:

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
1975–1976	2	13	16	21	8	7	17	5

One instance of moaning or roaring was heard each month in June, July, and August, but none was recorded in September.

The circumstances related to these calls appeared quite variable, but the calls sounded very similar in each case. One tigress moaned seven times after having been seen by sambar and chital; it was not known if she was hunting. Another tigress moaned nine times as she walked along with head held low, and 10 minutes later an animal moaned 15 times from the direction the tigress had gone. An adult male roared once while approaching a rest site, and two tigresses roared while apparently attempting to make a kill. Mutual roaring was also noted on several occasions. For example, on 15 November 1975 tigress 103, apparently in heat, was located on an island at the northeast corner of the park. At 0915 hrs 103 roared, another tiger about 100 m away then roared, and several exchanges were heard during the next 10 minutes. Presumably the other animal was the resident male (105), who had lost his radio-collar. On another occasion (15 February 1976) tigress 106 was located at a bait kill at 0710 hrs. Five minutes later she began calling, and 20 roars were heard in the next 15 minutes. Several roars were then heard from an uncollared tiger nearby. Number 106 left the bait kill, and by 0745 hrs she was about 0.8 km from the site. At 0740 and 0820 hrs an uncollared tiger roared twice from the bait site. Presumably her uncollared young had moved to the kill; 106 and two large young had been seen at this site on the previous day. At 0822 hrs the resident male (105) roared and then 106 roared; 105 was located about 0.4 km from the bait kill and at least 0.8 km from 106. Four more exchanges were heard in the next eight minutes, and then 105 left the area; by 0900 hrs 106 was inactive. Two months later, this same female was heard roaring from a grass area southeast of a guard station and another tiger, northwest of the station, began roaring, but only a few exchanges were heard.

Discussion

The demands of living in dense, broken terrain, where relatively small-sized prey are scattered and time-consuming to find has apparently not fostered, in most big cats and other carnivores, the development of complex social structures (Kleiman and Eisenberg, 1973). Under these conditions the most efficient method of locating and capturing prey appears to be by solitary individuals employing stalk and ambush hunting techniques (Schaller, 1967, 1972; Eisenberg and Lockhart, 1972; Seidensticker, et al., 1973; Hamilton, 1976). The problems of spacing have apparently been solved by behavioral mechanisms promoting dispersal, but there are occasions on which even a solitary animal must associate with other individuals for mating purposes, or while caring for young.

Tigers also socialize at kills, but in this study few associations were recorded at natural kills. Of the large groups reported in the hunting literature, the vast majority were observed either at bait kills or when forced out of cover at bait kills (Smythies, 1942; Powell, 1958; Perry, 1964). On one occasion Schaller (1967) observed six tigers walking together, but on seven occasions groups of six to seven were seen around bait kills. Aggregations of tigers have also been reported by McDougal (1977). At a newly established bait station he observed two or more tigers together on 59 occasions; on 25 of these three tigers were present and in 10 instances four were at the site. Most of these groups were composed of a female with one to two large young, but another adult female, and sometimes an adult male, were also present. These aggregations did not persist, however, but lasted only a few months.

It would seem that the chances of animals encountering others at regularly baited sites is higher than would occur at natural kills, especially if the sites are situated at the interface of home range boundaries; and data from this study suggest that tigers do not associate as frequently at natural kills as might be inferred from observations made at bait sites. The gatherings do indicate, however, that under special circumstances (e.g., large and steady food supply) tigers of various sex and age classes are capable of socializing. Schaller (1967) observed little sign of aggression at baits, and McDougal (1979) has recorded two or more adults at a bait kill on 88 occasions over a 6-year period with no serious confrontations. Outside of this situation, however, adult and independent tigers, like mountain lions (Seidensticker, et al., 1973), leopards (Eisenberg and Lockhart, 1972; Hamilton, 1976), and other solitary felids (Bailey, 1974; Berrie, 1973; Leyhausen, 1979), appear to socialize infrequently, and when they do their associations are apparently brief, lasting for only a few hours to perhaps several days at the most.

The only prolonged social contact in the tiger is that of a female and her dependent offspring. The young remain with the female until they are between 12–20 months of age (Schaller, 1967; McDougal, 1977; Panwar, 1979). In their second year the young spend progressively more time away from their mother, with young males tending to travel alone at an earlier age, until eventually they are nutritionally independent. They do, however, continue to use their natal areas for some time after becoming independent. A female (103) in Chitawan used her mother's range until she was about two years old, and her sibling brother (104) travelled in and out of the area until he was about 30 months old. Schaller (1967), McDougal (1977), and others have also observed young tigers remaining in their natal areas until two to three years old. A similar pattern has been reported for female black bears (Rogers, 1977) and young leopards (Muckenhirn and Eisenberg, 1973; Schaller, 1972; Hamilton, 1976; Bertram, 1978); although two sibling male leopards in Chitawan left their natal area abruptly after reaching independence at the age of about 15 months (Sunquist, in prep.). An abrupt transition has also been reported in mountain lions, where the young leave the natal area within a few weeks of becoming independent (Seidensticker, et al., 1973).

The major reasons for adults not tolerating independent offspring would appear to be competition for food and mates. Where resources are scarce the presence of these offspring, simply by the extent of their nutritional requirements, places an additional strain on the female's ability to raise a new litter. However, where resources are abundant it may be that females can afford to tolerate the presence of these young, and by doing so increase the young's chances of survival, and their own reproductive success.

By allowing their offspring to remain within the natal area for an extended period of time, adults may be allowing them access to important information as well as a known and reliable food supply when they are not yet experienced hunters. Young may learn what constitutes a suitable home range area, hunting techniques, behavior during interactions with the opposite sex, as well as the suitability of various den sites. It is interesting to note that on two occasions subadult male 104 was located within 200–300 meters of his mother and the resident male during periods of suspected sexual activity. In addition, when 101 gave birth to a new litter, 103, her subadult daughter of a previous litter, was present; in fact it was one of a very few occasions on which they were together after 103 became nutritionally independent. After reaching sexual maturity, 103 appropriated her mother's home range, and used the same den site to give birth to two of her own litters (Tamang and Smith, pers. comm.).

In this situation, where the young remain in the natal area for some time after reaching independence, the likelihood of a female offspring acquiring its mother's home range is probably increased as the female's movements are restricted with the birth of a new litter. Such a range appropriation was observed on one occasion during this study (involving 101 and 103), but under the circumstances involved there was no reason to assume that 103 had inherited her mother's range; a behavior that has been suggested to occur in bears (Herrero, 1978), sloths (Montgomery and Sunquist, 1978), squirrels (Smith, 1968) and others (Greenwood, 1980). McDougal (1977) has recorded no instance of daughters inheriting portions of their mother's range, although daughters are known to have established territories adjacent to their mothers. Panwar (1979) has, however, noted one instance of a daughter acquiring her mother's territory, and, as in this study, the mother established a new territory in an adjacent area and continued to have young. The circumstances associated with the range shift noted by Panwar (1979) are not known, nor is it known if these females would have behaved differently toward unrelated female offspring, but if adjoining areas are unoccupied and suitable the advantage to a female shifting to accommodate her daughter is clear as by doing so she maximizes her genetic contribution to the population. This situation does, however, increase the possibility of inbreeding, and in relatively small localized populations, in which tigers currently exist, this could lead to reduced viability of young (Ralls, et al., 1979), and thus one would expect there to be pressure on offspring to disperse from their natal areas and to establish ranges elsewhere.

The second most frequently encountered association was that of an adult male with adult females. However, females with small young were not found to associate with adult males. McDougal's (1979) observations from regular bait stations show that females with small young rarely visit bait sites and are consistently more wary than are females with large young or no cubs. My observations show that in addition females with small cubs tend not to stay with a bait kill but would lie up some distance away. No instances of males killing cubs were recorded during this study, but McDougal (1977) has recorded two cubs less than a year old being killed by an intruding male at a bait site, and Panwar (1979) describes two instances in which cubs were killed by a male. All these observations suggest that small cubs are particularly vulnerable and that there is pressure on females to avoid situations where other tigers, especially males, may be encountered.

The potential danger to cubs from intruding males is likely reduced by virtue of a female's range being included within the larger range of a male. Adult males have not been observed to share home ranges, and while transients may occasionally be seen in a resident's area, they do not remain long (Schaller, 1967; McDougal, 1977). The exclusion of other adult males would benefit the resident by reducing the possibility of infanticide; and while males are not directly involved in providing food for young, the mere exclusion of others reduces competition for females that must kill at a higher rate to provide food for growing young. It would also be adaptive for males to assume different feeding habits from females (Geist, 1971a). The limited data available indicate no separation between the sexes, either in size of prey taken or the times of day when animals are active, but males and females in Chitawan do show significant seasonal differences in habitat use (Table 8). This may serve to reduce competition between the sexes for food.

Males will mate with any estrous female encountered and thus by maintaining as large an area as energetically feasible, a male can increase the number of females with which he can potentially mate. For example, male 105 expanded his range when the opportunity arose and thereby doubled the number of females in his range (J.L.D. Smith, 1978); within one year he (105) impregnated six tigresses and possibly a seventh (McDougal, 1979). A male's chance of a successful mating may also be increased by being familiar with tigresses and their habits (Zajonc, 1971); as this may reduce tension during the potentially dangerous mating circumstances (Ewer, 1974).

Females, however, can maximize their reproductive success only by rearing young to adulthood. The birth of young is a critical time, not only because small cubs require attention, but the female must later secure the food for herself and her young. In this regard, it has been suggested that familiarity with an area is important in terms of hunting success, a factor affecting females more than males (Seidensticker, et al., 1973). Thus, in areas of prime habitat, one would expect competition between females for home ranges to be high, and that female ranges within these areas would be stable, whereas the ranges of males would tend to expand and contract as neighboring males competed for more females.

Of importance in this regard is how tigers maintain their spatial distribution patterns and regulate the social interactions within their respective areas. I found no evidence of active defense of territories, although J.L.D. Smith (1978) has since recorded fights involving some of the same animals I monitored. Fights between males over estrous females have been reported (Baikov, 1925), but damaging encounters would seem maladaptive, as an injured animal may starve to death unless alternative and easy prey are available. Defense of territory need not, however, involve fighting and in many large mammalian carnivores the exclusive use of areas is maintained without frequent antagonistic encounters (Mech, 1970; Schaller, 1972; Kruuk, 1972; Seidensticker, et al., 1973; Hamilton, 1976; Herrero, 1978). As pointed out by Geist (1971a), unless an animal can obtain enough energy over that required for maintenance and work, it will become a reproductive failure. A solitary predator, unlike a pack animal, relies on its physical well-being to secure food and thus cannot afford a serious injury (Ewer, 1973; Hornocker, 1969).

So, while fighting may occasionally occur, it is not likely to be the principal mechanism for promoting or maintaining the spatial patterns observed in tigers. Schaller (1967) noted a self-limiting trend in tigers, as the number in his study area did not increase when prey was concentrated during several months of the year. He suggests that this spacing was possibly based on intra-specific intolerance or subtle visual and olfactory signals left in the environment.

Both sexes deposit scent marks in the form of urine, and possibly anal gland secretions, throughout their ranges at all times of the year. As the spray commonly strikes objects about one meter above ground, dispersal of odor by wind would be facilitated; and according to the diffusion model of Bossert and Wilson (1963), a point source above ground can produce a scent field twice as large as a source at ground level. The odor of the scent is also persistent, as it is fixed in the form of lipids (Brahmachary and Dutta, in press). Schaller (1967) suggests that both feces and scrapes have communicatory functions, but the prominence of each depends on the season, with scrapes being more common in the wet season, when feces quickly disappear. A higher incidence of scraping in the wet season has also been reported for leopards in Sri Lanka (Eisenberg and Lockhart, 1972). Tree scratching is likely to be another mode of communication (McDougal, 1977), although I found no evidence of this behavior. Any disturbance to the substrate or other objects could attract attention and thus serve as a visual signal to olfactory information, an important consideration for a visually oriented animal. The occurrence of these scent-marking patterns in tigers and most other solitary felids attests to their communicative importance (Table 19; see also Wemmer and Scow, 1977; Verberne and Leyhausen, 1976), and likely function as spacing mechanisms, although there are sexual and species differences in the expression of these behaviors. Wemmer and Scow (1977) conclude that in the *Felidae* feces do not have the communicative significance of that in canids, but urine is undoubtedly an important carrier of information. What information is potentially being transmitted via urine and possibly other exudates most likely includes individual identity, sex, reproductive condition, and the time the mark was made (Ewer, 1973; Seidensticker, et al., 1973; Eisenberg and Kleiman, 1972). As this information is deposited along the network of commonly used trails it could certainly serve to indicate that an area is occupied, and possibly that within the marked area certain rights and privileges are claimed by the marking animal. There is, however, as pointed out by Ralls (1971), little evidence to support the view that scent marks lead recipients to avoid areas, and the occasional presence of transients in occupied areas shows this to be true in tigers. They do not, however, remain there long, suggesting that they may be at a disadvantage. Evidence summarized by Johnson (1973) for lagomorphs and rodents indicates intruders entering a marked area modify their behavior, tending to be more cautious and ready to withdraw on sighting a resident. Similar observations have been made of leopards (Hamilton, 1976) and wolves (Peters and Mech, 1975) when they were in another animal's or pack's territory. Whether these behavioral changes are in response to previous adverse encounters, alien scent marks, unfamiliar terrain, or to the absence of the intruders own scent marks is not known, but all are probably important in orienting and regulating the spatial and social relationships of individuals.

No resident tiger in this study was found in the territory of a like-sexed adult, at least not while the other was alive; although female 101 was located in another female's range shortly after she (101) "lost" her territory and, as such, she could be considered a transient. Interestingly, on two occasions this same female (101) was followed while she moved along the presumptive territorial boundary of her daughter's (103) range. She did not enter the area though it was not unfamiliar terrain since it was formerly her territory. In the first case avoidance may have been related to the daughter's presence, both were located at the same point within 15 minutes of each other. In the second instance, which occurred a month later, the daughter was not in the immediate vicinity but she had been located along this boundary four days earlier. McDougal (1977) has found resident females in the territories of other females but they did not use an area at the same time; it was only when an area was not used by the resident that another female moved in. Resi-

TABLE 19.—Some patterns of indirect and long-distance communications in nine felids (+ = present; +/− = observed but appears to be infrequent; ? = unknown, possibly present; − = absent)

Species	*Urine spraying*		*Feces*	*Scraping (scuffing)*		*Tree scratching*	*Long-range call*	*Source*
	M	*F*		*M*	*F*			
Lion	+	+/−	Scattered, uncovered, not associated with scrape	+	+	+	+	Schaller, 1972; Bertram, 1978
Tiger	+	+	Scattered, uncovered, sometimes associated with scrape	+	+	+	+	Schaller, 1967; McDougal, 1977; this study
Leopard	+	+	Scattered, uncovered, rarely associated with scrape	+	+	+	+	Eisenberg and Lockhart, 1972; Hamilton, 1976; R. M. Smith, 1978
Mountain lion	−	−	Scattered, covered and uncovered, sometimes associated with scrape	+	+	+	−	Seidensticker, et al., 1973; Schaller and Crawshaw, 1980
Snow leopard	+	+	Scattered, uncovered, sometimes associated with scrape	+	+	?	+	Schaller, 1977; Hemmer, 1972; Wemmer and Scow, 1977
Jaguar	+	?	Scattered, uncovered	?	?	+	+	Scaller and Crawshaw, 1980; Fiedler, 1957
Bobcat	+	+	Scattered and localized, covered and uncovered, sometimes associated with scrape	+	+	+	−	Provost, et al, 1973; Bailey, 1974; Young, 1958
Lynx	+	+	Scattered and localized, covered and uncovered	+	+	?	−	Saunders, 1963; Berrie, 1973; Berrie, in Leyhausen, 1979
Cheetah	+	+/−	Scattered, uncovered, rarely associated with scrape	+	+	+	−	Schaller, 1972; Eaton, 1974

dents probably know each other by scent, sound, and sight, and in the course of occasional encounters they have likely resolved their differences and waste little energy in hostile exchanges. Encounters with strangers, however, may not be without conflict, as shown in observations on domestic cats (Leyhausen, 1965). This apparent mutual avoidance (male vs male; female vs female) does not mean that residents never enter adjoining territories, and the quickness with which vacant or unused areas are occupied suggests that probes into neighboring areas are regular occurrences, but intruders do not remain long in occupied territory.

An additional potential spacing mechanism is the long-range call, although tigers do not appear to be very vocal animals (Schaller, 1967; McDougal, 1977; this study). The limited data do indicate that roaring and moaning are important in a variety of contexts, most of which are affiliative. Cubs have moved to their mother after she called, suggesting they recognize her call (Schaller, 1967; McDougal, 1977); and tigers reportedly roar after killing a large animal, giving the impression it is drawing attention to an ample food supply (Champion, 1927; Schaller, 1967). Roaring is heard during mating (Sankhala, 1977), and in this study the roaring/moaning of a tigress in estrus coincided with visits by an adult male, suggesting its importance in mating situations. These roars and moans are resonant and can be heard over considerable distances (3.2 km), but in this study no animals were actually observed to respond to these calls. It may be, as suggested by Schaller (1967), that tigers living in an area know each other's calls and respond selectively, depending on the individual giving it, and possibly on the context of the call as well. In every case, however, the sound draws attention to the animal, making others aware of its presence and location; and in this sense it could function to maintain distance between individuals, as suggested for the long-range call of the leopard (Eisenberg and Lockhart, 1972; Hamilton, 1976) and lion (Schenkel, 1966; Schaller, 1972; Bertram 1978).

While spacing of individuals is apparently accomplished by scent-marks and long-range calls, these modes of communication also appear to be important in bringing animals together for mating purposes. Tigers of the opposite sex were found together on few occasions outside of periods of suspected sexual activity; and their associations were brief, the longest was 2 consecutive days. In about half of the instances a male's appearance coincided with a period of roaring/moaning by a female, while in the other half no calling was heard. However, only one tigress (103) was heard to call and these bouts were most likely associated with her first heat periods. An adult male visited her (103) during each of her first five heats (Table 17), once they engaged in a duet, and they were not found together at any time between these suspected heats, suggesting that the calling served to bring these two animals together. Urine-marking was not likely to have been involved in stimulating the male's interest because during her first heats 103 was living in a small area just outside the resident male's range, and he (105) had not been found in this area in the 10 months before she began calling, nor had any other adult male ever been found in this area during the study. The pair (103 and 105) were later found together at intervals matching the earlier pattern, but during these suspected heats female 103 was not heard to call. No young resulted from any of these associations (Table 17) but she did conceive three months later.

A sexually experienced female was not heard to call during suspected heats, but the male's presence and apparent changes in her (101) scent-marking behavior suggested sexual activity was involved in their associations. In this case the female's sexual condition was probably indicated by scent marks deposited throughout her range (Eisenberg and Kleiman, 1972). A higher frequency of marking was apparent between suspected heats, which, given the large range of the male and the frequency of his visits to this part of his range, may ensure his presence at the appropriate time. Tigresses were not observed to travel widely during suspected heat periods, as reported in Ewer (1973), thus detection of any estrous female is primarily up to the male.

During the suspected heat periods of two females (101, 103) the resident male's interest was also suggested by a change in his movement patterns. In May 1975, for example, male 105 visited the eastern third of his range more often and at shorter intervals than he had in the previous three months (Table 12), and these changes correspond to the suspected heat periods of female

101. Male 105 also visited frequently and at shorter intervals in March and April 1976, suggesting sexual activity, but it was not known if either 103 or 101 was in estrus. He was, however, located with both females at intervals that matched the suspected length of the estrous cycle (about 25 days). While none of his associations with either female during these times resulted in a birth, both conceived a few months later. Conception rates of tigers and lions are low (Kleiman, 1974); although it is also possible that no mating occurred or that his visits did not coincide with peaks of receptivity. The sudden departure of female 101 from 105 during the latter part of one suspected heat may have been related to her lack of receptivity. The mean length of heat periods in tigers is about seven days (Kleiman, 1974), and this incident occurred on what was thought to be the seventh day. No such behavior was detected during other heats, nor has it been reported by others, and thus the event is clearly subject to other interpretations.

The frequency with which the resident male (105) visits most parts of his range probably ensures that he detects and/or encounters any estrous females, although mating opportunities do not occur with any predictable regularity. This suggests that his visits are possibly also related to maintaining an "optimum odor field" (Eisenberg and Kleiman, 1972) in which he feels secure (Ewer, 1973). They suggest that any inbalance in this odor field, due to the introduction of foreign scent or to the dissipation of his own scent, for example, will result in the individual attempting to restore the balance. In wolves, however, areas frequently visited are marked more often, which, Peters and Mech (1975) theorize, is related to a positive-feedback stimulus. Neither the fading of odor of a mark nor the presence of an alien mark is necessary to stimulate re-marking. The distribution of scent marks is thus related to repeated use of travel routes, some of which are marked more often.

The stimulus for marking in tigers is unclear, but it is evident from other studies (Eisenberg and Kleiman, 1972; Ewer, 1973) that this behavior could be related to many factors, including fear, anxiety, sexual activity, dissipation of personal odor, the odor of a conspecific, or possibly any novel scent or circumstance. A hand-reared free-living tigress, for example, scent marked at a higher frequency when entering unfamiliar terrain and upon re-entry into her domain (Choudhury, 1977); a tigress in this study marked at a higher rate between suspected heat periods. J.L.D. Smith (1978) also noted that two resident males marked intensively in an area where their ranges overlapped slightly. Just these few examples indicate there are likely to be many stimuli that release scent-marking behavior in tigers; and hence these marks, alone or in conjunction with other sign (scrapes, scratchings), could also serve multiple functions in the context of spacing, orienting an individual's movements, or integrating social and reproductive behavior. Similarly, the long-range call may serve a function(s) in these contexts, but as tigers call infrequently its importance for spacing appears to be limited.

The social system of the tiger is nevertheless one of dispersion in space and time. Except when modified by sexual activity or care of young the tiger is essentially solitary. It is capable of socializing, as behavior at kills indicates, but the constraints imposed by a closed habitat and the nature and distribution of the prey makes reduction of interference desirable and spacing allows for a more economical and less disruptive use of resources. In addition, such a system provides for the protection of young and ensures mating opportunities. Spacing and social integration of activities are probably maintained by a variety of sensory modalities, acting along or in concert.

Feeding Ecology

KILLING TECHNIQUES

METHODS.—The tiger's method of killing prey was inferred from the wounds on 13 wild ungulate and 13 bait kills. Baits were routinely weighed and ungulate weights were estimated from animals captured in tagging operations (see "Prey

Table 20.—Killing methods in relationship to the weights of prey and tigers

Age and sex of tiger	*Body weight of prey (kg)*	*Body weight of tiger (kg)*	*Weight ratio prey/tiger*	*Killing method*
Adult F	32[a]	143	.224	nape bite
Adult F	46[a]	152	.303	nape bite
Adult M	91	227[b]	.401	nape bite
Adult M	95	227[b]	.419	nape bite
Adult M	100[a]	227[b]	.440	nape bite
Adult F	85	159	.516	nape bite
Subadult M	84	160	.525	throat bite
Adult M	105	200	.525	nape bite
Subadult F	64[a]	114	.561	throat bite
Subadult M	90	160	.563	throat bite
Subadult M	91	160	.569	throat bite
Adult F	91[a]	159	.572	throat bite
Adult F	95	143	.664	throat bite
Adult F	102[a]	152	.671	throat bite
Subadult M	125	160	.781	throat bite
Subadult F	90	114	.789	throat bite
Adult M	182[a]	227[b]	.802	throat bite
Adult F	114	130	.876	throat bite
Adult M	177	200	.885	throat bite
Adult F	145[a]	159	.912	throat bite
Subadult M	148[a]	160	.925	throat bite
Adult M	227[a,b]	227[b]	1.000	throat bite
Adult F	140[a]	130	1.077	throat bite
Adult F	159	143	1.112	throat bite
Adult M	318[a,b]	227[b]	1.401	throat bite
Adult F	227	130	1.746	throat bite

[a] Wild ungulates.

[b] Scale only weighed to 227 kg (500 lb).

Size"). Ungulate kills were also weighed for comparison with estimated weights. The individual that made the kill was known, and body weights of tigers were obtained at the time of capture.

Results.—While sample sizes are not large, the data (Table 20) suggest that when the weight of the prey is more than half that of the tiger it uses a throat bite to kill. Kills were not dissected to determine whether the canines had severed or crushed the vertebrae, but in several cases involving a throat bite the trachea was crushed and no bone or bone splinters were felt by inserting my fingers into the bite holes, suggesting that the canines had not reached the braincase or the vertebrae. In contrast, bone splinters were usually felt when a nape bite had been used, suggesting damage to the vertebral column probably caused death; although the cause of death from either bite was not definitely determined.

Behavior with Kills

Tigers did not feed on kills at bait sites but dragged them into dense cover. The mean distance from kill site to feeding site was 125 m (range, 30–600 m, N=34). For eight natural kills there was no evidence of a drag, and in four other instances kills were taken about 75 m.

For both bait and natural kills (N=39), a single tiger, without exception, began feeding on the rump. As more of the carcass is eaten, the abdominal cavity is opened, and the digestive tract is pulled out. The eviscerated carcass is then dragged a few meters, and feeding continues until only pieces of skin and large bones remain. If the kill is large the tiger will often stay nearby ($\bar{x}$ = three days; range = two to seven days, Figure 31) until it has consumed the kill. In seven instances remains (skin, bones, little meat) of the kill were covered with grass. Both males and females showed this behavior. Occasionally the individual was relocated in the area of the remains but it was unlikely that anything remained as wild boar (*Sus scrofa*), jackal (*Canis aureus*), and jungle cat (*Felis chaus*) quickly scatter unattended kills.

FECAL ANALYSIS

Quantitative data on food habits of tigers were obtained by analyzing the contents of 55 feces.

METHODS.—Feces were collected when encountered during other activities. Tiger feces were distinguishable from leopard feces by their larger size and the usual presence of tracks.

To identify unknown hair in the feces a reference collection of hair of large mammals in Chitawan was established. Hair samples from the following species were included: sambar, chital, hog deer, barking deer (*Muntiacus muntjak*), gaur (*Bos gaurus*), domestic water buffalo, wild pig, rhesus (*Macaca mulatta*) and langur (*Presbytis entellus*) monkey, porcupine (*Hystrix indica*), hare (*Lepus nigricollis*), small Indian civet (*Viverricula indica*), large Indian civet (*Viverra zibetha*), binturong (*Arctictis binturong*), sloth bear, leopard, and tiger.

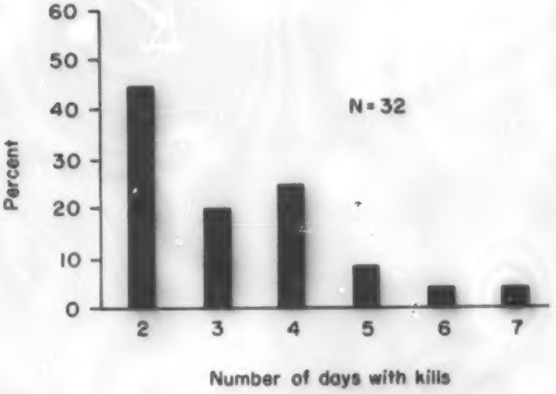


FIGURE 31.—Frequency distribution of time (days) tigers spend with kills.

Several fibers from each hair sample (known and unknown) were prepared by placing proximal, medial, and distal segments in Permount under a cover slip on a slide. Each sample was examined with a light microscope at various magnifications. Medullary patterns (Hausman, 1920) and root characteristics were drawn or photographed for comparison.

Several fibers from each known sample were also mounted on a SEM (scanning electron microscope) scanning peg, cross-sectioned, and then coated in a DC sputtering apparatus to 200 Å with gold-palladium. The coated specimens were viewed at 25 KeV in a JEOL (JSM 35) SEM equipped with a 200 μm objective aperture. Photomicrographs were taken of each sample at various magnifications. Variables investigated included width of hair, cuticular scale patterns, external and cross-section form of hair, and medullary characteristics.

The presence of identifiable items in each sample was recorded and their frequency of occurrence expressed as the percentage of the 55 feces. No attempts were made at more quantitative evaluation.

RESULTS.—Analysis indicated that most samples contained the remains of only one prey species. Deer hair was identified in 45 of 55 (82%) feces. Cervid hair was distinguishable from that of other species by the medullary patterns using only light microscopy (see Koppikar and Sabnis, 1976). Of the feces containing deer hair, 11 were identified as sambar on the basis of width and external form, the remainder (34) were probably chital and hog deer since barking deer do not appear to form a significant part of the tiger's diet. The hair of these three cervids could not be reliably distinguished by light microscopy or preliminary examination by SEM, even when several characters were used. Further analysis may indicate diagnostic differences between the hair of these cervids, but at this time results are inconclusive.

Soil and grass fragments were present in almost every sample, and two feces consisted almost entirely of soil, suggesting deliberate earth-eating, as noted also by Powell (1958) and Schaller (1967).

The hair from two samples have not been identified, and several species occurred infrequently, including wild pig, monkey (possibly langur), domestic livestock, and a civet (probably binturong based on claws in sample). For comparison, the frequency of occurrence of mammalian species in tiger feces from Chitawan and Kanha Park is shown in Table 21.

NUMBER AND SPECIES OF PREY KILLED

A further attempt was made to determine the food habits of tigers by collecting data on kills. Kill data were jointly collected by myself and K. M. Tamang. Some kill data were collected from the same area by Seidensticker (1976a), and are included in Table 22.

METHODS.—Kills by radio-tagged tigers were found through examination of suspected kill sites after the tiger's departure, and by pushing tigers away from suspected sites. Suspected sites were indicated by departures from the normal movement pattern. Tigers were usually not located in the same place on consecutive days except when with small cubs or a kill.

The majority (38) of kills were discovered by radio-tracking tagged animals. Eight were found accidentally, and 18 were obtained by following up reports from varied sources; in most of these 26 cases we were almost certain that tigers had made the kill. The few unknowns were assumed to be tiger kills since among the other likely predators present, wild dogs were rare, poachers usually remove the entire carcass, and leopards were common but primarily in riverine forest areas along the park's periphery. None of the prey animals necropsied were heavily parasitized, and there was no evidence that disease, starvation, or old age was the cause of death. Only kills from the northeast part of the park are included, since almost all location data were from this area.

RESULTS.—Twenty-eight suspected sites were examined after the tiger's departure, and a kill was found on 25 occasions. In one instance when a kill was not found, the smell of decomposed flesh was obvious, but the remains could not be

TABLE 21.—Frequency of occurrence of mammalian species in tiger feces

Species	*Kanha Park*[1]		*Chitawan Park*[2]		*Chitawan Park*[3]	
	No.	*%*	*No.*	*%*	*No.*	*%*
Gaur	28	9.3	–		–	
Swamp deer	29	9.7	absent			
Sambar	35	11.7	36	29.3	11	20.0
Chital	175	58.3	41	33.3	34	61.8
Hog deer	absent		19	15.4		
Barking deer	–		5	4.1		
Wild pig	3	1.0	13	10.6	2	3.6
Porcupine	9	3.0	1	0.8	–	
Hare	–		1	0.8	–	
Langur monkey	21	7.0	7	5.7	2	3.6
Cattle	–		–		1	1.8
Civet	–		–		1	1.8
Unknown	–		–		2	3.6
(Soil)					2	3.6
Totals	300	100.0	123	100.0	55	99.8

[1] Schaller, 1967.
[2] McDougal, 1977.
[3] This study.

TABLE 22.—Number and species of prey killed by tigers in Chitawan Park

Species	*1973–1974*[a]		*1974–1976*[b]		*Total*	
	No.	*%*	*No.*	*%*	*No.*	*%*
Domestic livestock	14	53.8	18	28.0	32	35.6
Sambar	4	15.4	20	31.3	24	26.7
Hog deer	3	11.5	12	18.8	15	16.7
Chital	2	7.7	9	14.1	11	12.2
Wild boar	2	7.7	4	6.3	6	6.7
Rhino calf	1	3.8	-		1	1.1
Barking deer	-		1	1.5	1	1.1
Total	26	99.9	64	100.0	90	100.1

[a] Seidensticker, 1976a.
[b] Sunquist and Tamang.

located. This method minimized disturbance but sometimes provided little information because scavengers were quick to scatter the remains, and dense cover made searching difficult. On other occasions, kills were found by pushing tigers away from suspected kill sites. Under these circumstances a kill was found on 13 of 14 instances. This method, while quite effective, may have disturbed the animal. Tigers that we pushed away were known to have returned to kills weighing 75 kg or more, but with smaller kills this was difficult to tell.

While searches of suspected kill sites indicated that 90% (38 of 42) of suspected kills were actual kills, it was only possible to search 47% (42 of 90) of all suspected sites. Dense cover made searches difficult and time consuming, and unless an animal's location was known precisely it was impractical to return and expect to find the remains, especially those of small prey. Imprecision in the tracking system precluded precise locations, except at close range.

Of the 64 tiger kills found in this study, 18 (28%) were domestic livestock (Table 22). Combined with Seidensticker's (1976a) data, livestock constituted about 35% of the kills in the northeast end of the park. Livestock kills were not, however, found to be equally distributed throughout this area; this is also evident from their low occurrence in feces. Of 18 kills, 14 (78%) were from one small area (4 km^2) and no kills of wild ungulates were found in this area. Similarly, the domestic livestock kills recorded by Seidensticker (1976a) were all from an area where we found few. This difference is related to the effectiveness of guards in keeping domestic livestock out of the park. These observations do indicate, however, that when livestock are available tigers readily prey on them. Leopards also readily take domestic animals (sheep, cow, goat, dog) if available; these prey constituted about 28% of kills of leopards residing in and around the northeast end of the park (Table 23).

Wild ungulates comprised about 64% of the tiger kills, compared to 85% recorded in feces; this difference is related to more domestic livestock in the kill data. Of the 42 deer killed, about half were sambar (20), and the remainder were hog deer (12), chital (9), and barking deer (1). Numerically, chital and hog deer are about 8 and 10 times, respectively, more abundant than sambar (Seidensticker, 1976b), suggesting that sambar are preferred prey and/or they are more vulnerable. However, sambar are three to five times larger than chital and hog deer (Figure 32), and thus require more time to consume. Small prey can be eaten in one to two days by a tiger, thereby increasing the likelihood that kills of young and small animals would not be discovered. This is evident from a comparison of fecal and kill data. The percentage of smaller cervids in feces was 62%, compared to 52% recorded in kill data, whereas the larger sambar comprised 48% of the kill data but only 20% of feces.

The percentages of prey in feces probably reflect more accurately the relative number of animals killed than does the kill data, although there are possible biases in both methods (Lockie, 1959; Kruuk, 1972). Small prey are relatively more hairy and therefore might be overrepresented in feces, and underrepresented in direct observation. These biases probably occur in the opposite direction for large prey. While neither method provides a totally satisfactory representation of the tiger's diet, taken together their opposite biases probably tend to cancel each other (Kruuk, 1972).

AGE OF KILLS

METHODS.—Thirty-five deer killed by tigers were aged by means of the eruption and wear on the premolar and molar teeth of the lower jaw. No animals of known age were available for comparison, so relative ages of chital and hog deer were established using the criteria of Robinette, et al. (1957) for mule deer (*Odocoileus hemionus*). The pattern of tooth eruption in chital is reported (Schaller, 1967:319) to be closer to mule deer than to white-tailed deer (*O. virginianus*). No information is available on the pattern of tooth eruption in hog deer, but it was assumed to be similar to chital, a congeneric species. Relative ages of sambar were established using the criteria for elk (*Cervus canadensis*) as described by Quimby and Gaab (1957). The pattern of tooth eruption in sambar is reported (Schaller, 1967) to be similar to that of elk. All kills were found in an area of about 20 km^2, thus the rate of tooth wear within a species was thought to be equal.

Age estimates based on cementum annuli counts (Low and Cowan, 1963; Gilbert, 1966) were compared with estimates based on tooth eruption and wear. Berwick (1974) concluded there was good agreement between these two methods for aging chital and sambar; although considerable differences are reported from the application of these methods to aging white-tailed deer (Hackett, et al., 1979; Cook and Hart, 1979). Tooth sections were commercially prepared, and annuli counts were made by myself and an associate, who was well acquainted with the method. When differences occurred between our counts, the range of the estimate was used.

RESULTS.—Tigers killed animals over a broad range of age classes (Table 24), suggesting that age was not a factor influencing vulnerability. Sambar of most age classes were represented in the kill data, and the 3–9-year-old animals are probably young to prime adults. Only the teeth of the two 15-year-old sambars were badly worn. Most of the hog deer kills were classified as yearlings and a few animals were judged to have been prime adults. Similarly, most of the chital kills were classified as young to prime adults. Fawns

TABLE 23.—Number and species of prey killed by leopards in Chitawan Park

Species	*1973–1974*[a]		*1974–1976*[b]		*Total*	
	No.	*%*	*No.*	*%*	*No.*	*%*
Domestic animals	2	14.3	10	34.5	12	28
Chital	4	28.6	7	24.1	11	26
Hog deer	4	28.6	3	10.3	7	16
Sambar	3	21.4	2	6.9	5	12
Barking deer	1	7.1	3	10.3	4	9
Wild pig	–		3	10.3	3	7
Vulture	–		1	3.4	1	2
Total	14	100.0	29	99.8	43	100

[a] Seidensticker, 1976a.

[b] Sunquist and Tamang.

FIGURE 32.—Major prey species in Chitawan: *a*, larger sambar; *b*, medium-sized chital; *c*, smaller hog deer.

of both species are poorly represented in the kill data and this is related to their size. Tigers can easily consume a young chital or hog deer in a day, and thus these kills would not be discovered. None of the hog deer or chital kills had teeth that were badly worn. No dental malformations, necrosis, or other deformities were noted in any of the deer killed.

Prey Size

Few animals appear to be immune to tiger predation. Adult rhino and adult gaur are rarely killed (Figure 33), but tigers occasionally killed herbivores that were considerably larger than themselves. Most of the prey killed by tigers weighed about 50–100 kg, but animals the size of adult sambar and domestic buffalo (160–400 kg) were regularly taken, and the occurrence of monkey hair in feces indicates very small prey are also consumed. By comparison, most of the prey killed by leopards residing in the same area weighed about 25–50 kg, but there is considerable overlap in the size of prey taken by these predators (Table 25). An indication of the prey species likely to be represented in the various size classes is shown in Table 26.

Food Consumption

Methods.—Estimates of food consumed were obtained by several methods. The baits used in capture operations were routinely weighed; when a bait was killed the remains were weighed at varying intervals, thus providing an estimate of consumption over time. Weights of natural kills were estimated from animals captured as part of a tagging operation (Table 26); remains of natu-

TABLE 26.—Comparison between age estimates based on tooth eruption-wear and cementum annuli counts (in years) of ungulates killed by tigers (nd = no data)

Sambar		*Hog deer*		*Chital*	
Eruption-wear	*Cementum*	*Eruption-wear*	*Cementum*	*Eruption-wear*	*Cementum*
<1	1/2	1	1	1.5	[illegible]
1-1.5	nd	1	nd	1.5	1+
1-1.5	nd	1+	1	2	nd
1-1.5	nd	1.5	1+	2+	2
1.5	1+	1.5	1+	2.5	nd
2	nd	1-2	1+	3.5	4
3	nd	2+	2	3.5	5
3-3.5	3+	2.5	2	5.5	5+
7.5	7	3.5	3	5-6	6+
7-8	7	4.5	4		
7.5-8.5	nd				
8	6-11				
8	nd				
9	nd				
15	15+				
15	15+				

ral kills were also weighed. The body weights of both baits and wild ungulates were reduced by 30% to adjust for the weight of gut contents. This correction factor was determined from gut content weights of baits and natural kills.

RESULTS.—Estimates of the amount of food that can be eaten by a single tiger are shown in Table 27. The average quantity consumed in one day may be too low since most of this information was from animals that were disturbed at bait sites. On two occasions the tiger was known to be eating when we arrived. If the tiger is left undisturbed the average amount eaten in two days is more than double that of the first day, suggesting that the one-day value is low. A hungry tiger probably eats more on the first day of feeding than on successive days. For example, a tigress killed an adult female chital about mid-morning, and by the next morning only skin and bones remained. She had consumed an estimated 30 kg, or about one-fifth of her body weight. Similar estimates are reported by Schaller (1967). Larger kills, such as sambar and domestic buffalo provide food for several days and enormous quantities of meat are eaten (3-7 day values). Males also tend to eat more than females in the same time interval. In three days of undisturbed feeding an adult male consumed 56 kg; another adult male ate 57 kg in the same time. By comparison, a tigress fed for three days on an adult male hog deer that weighed 68 kg, eating approximately 41 kg. She also spent three days with each of two other adult male hog deer kills. Even large kills may not last long, however, if the kill is shared among several tigers. For example, a tigress accompanied by two large young consumed 102 kg in just two days, or about 17 kg/day per animal. On another occasion, a large domestic buffalo plus an adult cow were eaten in six days by four tigers. A large male fed on these kills for four days, he left, and a tigress with two large young fed for two days. These tigers had consumed an estimated 195 kg; all edible parts of the carcass had been eaten. It also became apparent during the hot season that tigers have no aversion to putrified meat. On two occasions, one in April and the other in May, a tiger ate for four and five days on a carcass that was rancid.

KILL RATE

METHODS.—Movement data were used to estimate the frequency with which tigresses (N=3) without young killed prey large enough to detain the predator for more than a day. Sample sizes for males were too small for analysis. Estimates were based on consecutive daily locations for 8-, 12-, and 19-day periods (non-overlapping); these incorporate both known (N=16) and suspected kills (N=17). Since an estimated 90% of suspected kills were actual kills, the number of suspected kills were corrected accordingly. Data obtained during periods of baiting were not included.

RESULTS.—The estimated frequency of killing by tigresses without dependent young varied from one every eight days to one every 8.5 days, or 42-45 kills/year (Table 28). Taking the error of the estimates into consideration, a tigress made 40 to 50 kills per year. A tigress in the same area with two 6-10-month-old young killed every five to six days, or 61–73 animals/year (Seidensticker, 1976a). By comparison, Shaw (1975) estimated that mountain lions with kittens made a kill every 6.8 days; females without young and mature male lions killed once every 10.4 days.

The rate of killing by both male and female tigers in the northeast end of the park is higher than necessary because of scavenging by local villagers and employees of the government elephant camp. In an 8-month period 10 kills were known to have been scavenged, including seven sambar, two wild boar, and one hog deer. In most cases the tiger had fed for one or two days on the kill before it was appropriated.

Discussion

Unlike coursing predators, the large solitary cats depend on concealment and a stalk and ambush approach to capture prey; and whereas a vulnerable animal is likely to be detected in a long chase, it would not necessarily be singled out for capture in a short rush from dense cover. In this situation any animal placing itself in a vulnerable position is likely to be taken. This hunting method probably influences the kind of prey killed. Kill data from this study showed that healthy animals of most sex and age classes were regularly taken, suggesting that age is not a factor influencing vulnerability. Similarly, tigers in Kanha Park regularly killed animals that were in good physical condition, including young to prime adults (Schaller, 1967).

The variability in cover suitable for stalk and/or ambush, seasonal differences in habitat affinities and group size, and pregnancy appear to affect an animal's vulnerability. Schaller (1967) noted that deer and antelope that tended to remain on burnt-over areas were rarely killed, but when cover had grown high these same species were again killed. Swamp deer hinds in an advanced stage of pregnancy also readily fell prey to tigers, apparently having lost some of their agility. In this study 12 of 19 sambar were killed from January to May, whereas few were killed between June and December. This difference may be related to cover, as beginning in January the grasslands are burned, and after the fires hog deer and chital forage in the open areas in large groups. This behavior may reduce their vulnerability and thereby increase the pressure on sambar. Relatively few hog deer and chital kills were found during this period. Differences in vulnerability of ungulates in different types of cover and terrain have been reported by Hornocker (1970) for species preyed upon by mountain lions and by Wright (1960), Mitchell, et al. (1965), and Schaller (1972) for those subjected to lion predation in Africa.

Tamang (1979) reports that chital and sambar males were taken out of proportion to their availability. If this is the case it suggests that males are less wary or more exposed, perhaps because they are more competitively active, and travel over wider areas than do females.

The techniques used by big cats to dispatch prey vary roughly according to the size of the animal taken. While I found tigers used a throat bite only on prey more than half their weight, McDougal (1977) observed that on a prey (bait) size of 70 kg males used a nape bite (18) more often than a throat bite (10), whereas females used both methods with about equal frequency (25 vs 24). He also notes that young tigers are not adept at killing, but with experience the bite changed from the throat to the nape on prey of this size. A nape bite is used by most cats on small prey (Leyhausen, 1965), although Schaller and Vasconcelos (1978) observed that jaguars commonly use a bite to the posterior part of the cranium to kill capybara (*Hydrochoerus hydrochaeris*), an animal much smaller than itself. Lions kill prey, depending on the size and species, with bites to the throat, nape, muzzle, and sacrum (Kruuk and Turner, 1967; Schaller, 1972; Eloff, 1964); leopards also use the throat and nape bite (Kruuk and Turner, 1967; Schaller, 1972; Hamilton, 1976). The techniques used by tigers and other large cats to kill prey are obviously variable and, as noted by Schaller (1967), even the same individual may use different methods in similar situations; but subduing prey is largely dependent

FIGURE 33.—Animals essentially invulnerable to predation by tigers, largely by virtue of their size: *a*, adult rhino; *b*, adult gaur

b

TABLE 25.—Size of prey killed (in kg) by tigers and leopards in Chitawan Park (data from Seidensticker, 1976a included)

Animal	*<25*	*25–50*	*50–100*	*100–200*	*200–400*
Tiger					
Wild species	-	15	19	13	11
Domestic stock	-	-	3	3	26
Leopard					
Wild species	8	15	7	1	-
Domestic stock	5	3	3	1	-

TABLE 26.—Weights of wild ungulates captured in Chitawan Park as part of tagging operation (scale only weighed to 227 kg (500 lb))

Species	*Age/sex*	*Weight (kg)*	*Capture date*
Sambar	adult M	227+	16 Jan 75
	adult M	227+	25 Feb 75
	adult M	227+	23 Jan 76
	adult M	227+	7 Apr 76
	adult F	193	6 Feb 75
	adult F	152	28 Jan 76
	adult F	180	8 Apr 76
Chital	adult M	61	14 Mar 75
	adult M	91	8 Apr 75
	adult M	91	21 Jan 76
	adult M	84	7 Apr 76
	adult M	93	8 Apr 76
	adult F	50	9 Apr 75
	adult F	61	15 Apr 76
Hog deer	adult M	39	11 Mar 75
	adult M	68	14 Apr 76
	yearling M	27	11 Apr 75
	adult F	36	9 Apr 76
Barking deer	adult M	25	18 Mar 75
	adult F	20	28 Feb 75

TABLE 27.—Food consumption of tiger feeding on baits and natural kills (s.e. = standard error)

Period	*Average consumed (kg ± s.e.)*	*Average consumed per day (kg)*
1 day (N=11)	14 ±1.6	14.0
2 days (N=13)	35 ±2.0	17.6
3 days (N=8)	46 ±2.3	15.3
4 days (N=4)	65 ±1.7	16.3
5 days (N=1)	86	17.2
7 days (N=1)	130	18.6

TABLE 28.—Estimated frequency of killing by tigresses without dependent young in Chitawan Park (s.e. = standard error)

No. of consecutive days located	*Mean no. of kills ± s.e.*	*Rate of killing*	*No. of kills/year*
8-days (N=14)	0.94 ±0.05	1 kill every 8.5 dys	42.9
12-days (N=6)	1.47 ±0.22	1 kill every 8.2 days	44.7
19-days (N=4)	2.35 ±0.29	1 kill every 8.1 days	45.1

upon relative prey size (Elliott, et al., 1977), and in this regard the throat is apparently the most effective and safe site to kill larger prey.

The feeding behavior of large cats show some interesting differences (Table 29). Tigers begin feeding on the rump, as also noted by McDougal (1977) and Schaller (1967); McDougal also reported that tigers first bite off the tail. If more than one tiger is present feeding begins on other areas as well as on the rump (Schaller, 1967). Similarly, mountain lions begin feeding on the rump (Hornocker, 1970), but lions usually start on the viscera (Schaller, 1972), and leopards begin on the viscera or the meat on the thighs or chest after occasionally plucking fur from the prey (Turnbull-Kemp, 1967; Schaller, 1972; Hamilton, 1976). Cheetah begin feeding on the thighs (Schaller, 1972), and jaguars tend to begin on the forequarters and chest (Almeida, 1976; Schaller and Vasconcelos, 1978). Since little of most kills is not eaten, it appears that some parts are preferred, or perhaps the site of initial feeding is that most easily cut open, although this seems unlikely given the similarities in dentition (Ewer, 1973). Eisenberg and Leyhausen (1972) suggest that orientation to a feeding point in mammalian predators may be guided by moist areas or ori-

TABLE 29.—Behavior of large cats with kills

Species	*Initial feeding site*	*Stay with kills*	*Cover remains of kills*	*Source*
Tiger	rump	yes	yes	Schaller, 1967; McDougal, 1977; this study
Mountain lion	rump	yes	yes	Hornocker, 1970
Lion	viscera	yes	yes	Schaller, 1972
Leopard	viscera, thigh, chest	yes	yes	Turnbull-Kemp, 1967; Schaller, 1972; Hamilton, 1976; R.M. Smith, 1978
Jaguar	forequarters, chest, neck	yes	?	Almeida, 1976; Schaller and Vasconcelos, 1978
Cheetah	thigh	no	yes	Schaller, 1972; Adamson, 1969
Snow leopard	chest, lower abdomen, thigh	yes	?	Schaller, 1977

fices, which in some cases is also the site of the killing bite.

Most of the large cats remain in the vicinity of their kills until they have consumed them. The cheetah, however, is an exception: it eats rapidly, and then leaves, sometimes for no apparent reason (Schaller, 1972). Schaller and Vasconcelos (1978) did not observe jaguars staying with kills, or covering the remains. They suggest this may be because prey were common in the area. The behavior of covering remains of kills has been observed in many canids and felids, but in the latter its frequency of occurrence is highly variable and thus may depend on such circumstances as visibility, number of scavengers in the area, prey size, and number of animals feeding.

Tigers are capable of eating prodigious quantities of meat in a relatively short time. Schaller's (1967) work indicated that an adult tiger can readily consume 18–27 kg of food in a night, and McDougal (1977) reported that a large male ate 35 kg of meat in one night. Similar amounts were consumed in one night by males and females on a few occasions during this study, but the average amount eaten by one animal over several days was 15–18 kg/day (Table 27). This strategy of gorging permits utilization of large food items that are obtained on an intermittent basis and cannot be stored. A similar strategy is employed in feast or famine situations by hyenas (Kruuk, 1972), lions (Schaller, 1972), wolves (Mech, 1970), mountain lions (Hornocker, 1970), and others.

The large amount consumed in the short-term does not, however, indicate what the animal needs in the long-term. To maintain zoo tigers in a healthy condition requires, depending on the animal's sex and size, about four to eight kg/day (Schaller, 1967:324). While free-ranging tigers are on the whole more active than captives, in some respects the energy output in both situations is probably similar (Schaller, 1967). He suggests that in Kanha Park, where prey are abundant and ranges relatively small, tigers need five to seven kg/day. In Chitawan, tigresses make an estimated 40–50 kills/yr, spend an average of three days with each kill (Figure 31), and in three days of feeding consume an average of 46 kg (Table 27), the quantity of meat consumed in a year is therefore an estimated 1840–2300 kg. Thus, on a daily basis, tigresses ate five to six kg, or about the same amount fed to zoo tigers. The larger males would presumably eat six to seven kg/day.

However, approximately 30% of each prey carcass is comprised of inedible parts, so to obtain the required amount of mean (1840–2300) a tigress would have to kill an estimated 2629–3286 kg/yr. A male, assuming he requires six to seven kg/day, would need to kill about 3129–3650 kg/yr. In contrast, Sankhala (1977:39) figures a tiger needs to kill 4900 kg/yr, but his calculations assume a tiger requires 10–12 kg/day. Figures from this study more closely approximate those of Schaller (1967) and Novikov (1962); they estimate a tiger needs to kill 2844–3555 kg/yr and 3000 kg/yr, respectively. These figures indicate the minimum and presume that each carcass is completely utilized, which is sometimes not the case due to disturbance or scavenging. A few kills were scavenged by villagers at Chitawan, thus increasing the kill rate somewhat, but outside of these situations tigers appeared to utilize each kill and since kills of small prey are not likely to be detected, this probably offsets losses due to villagers. On the basis of these considerations, I feel that 2600 to 3300 kg/yr is fairly representative of the amount killed by each tigress, and with approximately 3100 to 3700 kg/yr by each male.

To compute the total amount of prey biomass required per year the total number of tigers must be considered. For the sake of simplicity, only the tiger population in Chitawan at the beginning of 1976 will be used. At that time there were an estimated three adult males, 12 adult females, and 14 young. The latter included two subadult males, two subadult females, six large young, and four small cubs. Subadults are nearly full-grown and probably require the amount of an adult; and assuming each large young requires half as much as an adult (Schaller, 1967), they were equivalent to three adult females. The four small cubs probably require the equivalent of one adult female. Seidensticker (1976a) found that a tigress with two 6–10 month-old young killed every five to six days or 61–72 animals/year; whereas tigresses in the same area without young killed an estimated 40–50 prey/year. The differences in these rates suggest 30%–40% more prey must be killed to feed two young of this age, and as some domestic buffalo (larger than average size prey), were also taken by this tigress, each young presumably required about one-fourth of that for an adult female. Based on these estimates, the equivalent of five adult males and 18 adult females were present, and would require from 65,300 to 77,900 kg of large prey animals per year. A few transients were also seen in the park, and as the number of resident females is a conservative estimate, the minimum prey biomass required is about 65,000 to 80,000 kg/yr.

An assessment of the impact of tiger predation on the prey populations can be made by evaluating the above figures against Seidensticker's (1976b) and Tamang's (1979) density estimates of wild ungulates in Chitawan (Table 30). There is a sizeable difference between their estimates of ecological biomass that is related primarily to the seasonal concentration of rhinos, but otherwise their figures are fairly similar. In comparison with other areas in India and south Asia containing similar faunas, the figures for Chitawan are exceeded only by Kaziranga, another alluvial plain environment also supporting large numbers of rhinos (Eisenberg and Seidensticker, 1976). However, rhinos contribute little to the diet of tigers, and to describe the available biomass it is appropriate to recalculate by excluding rhinos. Thus, in Chitawan the crude biomass available to tigers is an estimated 1222–1946 kg/km^2 and when extended over the park (544 km^2) the figure comes to 664,760 kg to 1,058,624 kg. The tigers in the park require an estimated 65,000 to 80,000 kg/yr, or about 8%–10% of the standing crop. When combined with that taken by leopards the amount removed is probably similar to that of carnivores in East Africa. In the Serengeti, lions remove about 4.6–5.5% of the estimated biomass and that removed by all the large predators, including lions, is roughly 9%–10% (Schaller, 1972:397). Tigers are, however, probably not taking 8%–10% of the available wild ungulate biomass because predation on domestic livestock is not included in these calculations. The density of livestock in the park is not known, but in some areas they contribute a large amount to the tiger's diet. Gaur, which are also not included in these figures, may be taken as well, but their numbers appear to be low, and they probably contribute little to the support of tigers in Chitawan. However, even without the biomass contribution of rhino, gaur, and domestic livestock, Chitawan supports about 1 kg of tiger to 390–630 kg of prey, which is similar to predator-prey biomass ratios observed in Africa (Schaller, 1972:396). This assumes the average density of adult tigers in the park is one per 36 km² (Table 5), and the average live weight of tigers is 111 kg (3/4 of average weight of adult females, Schaller, 1972: 454), for a crude biomass density of 3.1 kg/km². The ratio would, of course, be less if young were included.

The effect of predation on prey populations in Chitawan is difficult to assess, given the limited data available on ungulate densities and changes in the structure of these populations. Numerical and biomass density of most prey species appear to have increased slightly between 1974–1977 (Table 30); while the resident tiger population has remained fairly stable. This suggests that predation has been ineffective in limiting prey numbers. However, at another level, changes in the sex and age ratios of herbivores indicates differential mortality in chital and sambar, with males apparently being more vulnerable (Table 31). In Kanha Park, Schaller (1967) also noted selective predation on adult male sambar, but not on male chital. The kill data also show sambar to be highly preferred prey (Tamang, 1979; this study), but this is biased because kills of large-sized prey are much more likely to be found. Selective predation on adult males should, however, have relatively little effect on reproductive rates, as the deer are polygamous; and a reduction in the number of males might increase food availability for conspecifics. Nevertheless, the number of sambar young appear to have to decreased between 1974–1977. By comparison, the number of chital young have apparently increased, while hog deer and barking deer show little change in population structure. Wild pigs were severely reduced in number by an unknown disease in 1974, but their numbers are now increasing rapidly.

While there has been no systematic monitoring of vegetation in the park, it does appear that the effects of annual burning on the grasslands has been to maintain or improve them. Thus, conditions for grazers such as hog deer and chital have possibly become more favorable. Seidensticker's (1976b) and Tamang's (1979) density estimates

TABLE 31.—Age and sex ratio of large herbivores in Chitawan Park

Species	*Dec 1973–Apr 1974*[a]			*Jan 1975–May 1977*[b]		
	Male :	*Female* :	*Young*	*Male* :	*Female* :	*Young*
Chital	115	100	28	54	100	48
Hog deer	51	100	24	40	100	25
Sambar	102	100	50	55	100	22
Barking deer	74	100	11	78	100	13
Wild pig	30	100	38	93	100	180

[a] Seidensticker, 1976b.

[b] Tamang, 1979.

TABLE 30.—Estimates of numerical and biomass density of wild ungulates in Chitawan Park (data from Seidensticker, 1976b, and Tamang, 1979 (in parentheses))

Species	*Average weight (kg)*	*Ecological density (N/km²)*	*Crude density*	*Ecological biomass (kg/km²)*	*Crude biomass*	*Percent contribution to crude biomass*
Rhino	1410 (1340)	11.2 (2.1)	0.32 (0.43)	15792 (2814)	451 (643)	27 (24.8)
Wild pig	61.8 (45)	5.8 (4.8)	1.1 (2.9)	358 (216)	68 (131)	4.1 (5.1)
Barking deer	12 (17)	6.7 (7.7)	3.3 (6.6)	94 (131)	46 (112)	2.7 (4.3)
Chital	54.8 (54)	17.3 (18.6)	10.1 (16.8)	948 (1004)	553 (907)	33.1 (35)
Hog deer	31 (33)	35.0 (33.0)	5.5 (7.9)	1085 (1089)	171 (261)	10.2 (10.1)
Sambar	153.6 (198)	2.9 (3.0)	2.5 (2.7)	445 (594)	384 (535)	23.0 (20.7)
Totals		78.9 (69.2)	22.8 (37.4)	18722 (5845)	1673 (2589)	

and sex and age class data of sambar were collected primarily from riverine forest areas in the northeast section of the park. In contrast to the grassland, the suitability of this riverine habitat may have been qualitatively reduced by burning, combined with foraging by domestic elephants and the increased impact of tourism (more elephant tours). No obvious signs of nutritional stress were evident in the prey killed by tigers, but without information on rates of reproduction and/or recruitment the reasons for the decline of sambar young are unclear.

The broad prey base available to predators in Chitawan probably dampens the effect on any single species, but the picture is further complicated by differential seasonal vulnerability of the prey. During the latter part of the cool and early part of the hot seasons hog deer and chital congregate in large groups on the open burned grasslands to take advantage of the new growth. Relatively few kills of these species were found at this time, suggesting they were less vulnerable. Correspondingly, the predation pressure on forest-dwelling species is likely to be increased, and more sambar kills were found during this period than at other times of the year. Both sambar and wild boar are essentially forest species, and prior to the "crash" in wild boar numbers, these two species probably shared the brunt of predation when other prey were not as available. During the time wild pig numbers were low the pressure on sambar was probably increased. If this is the case, then one would predict that the effects of predation on sambar would be dampened as wild pig numbers increase and over time, the sambar population should recover; assuming of course that habitat conditions are favorable.

Overall, the high carrying capacity of the floodplains, combined with the multiple prey base, makes it unlikely that predation alone could have a long-term limiting effect on ungulate populations in Chitawan. However, a combination of changes in environmental circumstances could have short-term effect, as predation accounts for most ungulate mortality, and thus any increase in vulnerability can result in significantly greater mortality. In this way predation is capable of altering prey population levels, albeit ultimately habitat conditions and other factors should limit prey populations.

The Comparative Socio-Ecology of Lions and Tigers

The last radiation of the *Panthera* took place in the early Pleistocene and led to three closely related species: the lion, jaguar, and leopard; the evolutionary line to the tiger and the snow leopard diverged from the main stem of the *Panthera* earlier (Hemmer, 1978a). The earliest known fossils of the subgenus *Tigris* occur in southeast Asia (Java) in the Lower Pleistocene, and, according to Hemmer (1979a:59), "The present fossil remains of this tiger show no other distribution than that known from the Holocene [Recent]." This suggests either that the tiger originated in the forests of southeast Asia and did not radiate to its present geographical distribution until Recent times, or that older fossils are yet to be discovered.

On the other hand, fossil evidence suggests that the evolutionary center of the lion is to be found in the Lower-Middle Pleistocene of Africa; and by the Upper Pleistocene, records indicate that the lion was distributed throughout the open landscapes of Europe, southern Asia, Siberia, North America, and northwestern South America (Hemmer, 1979a). However, a rapid distributional decline of the lion occurred in the holarctic at the beginning of the Holocene as the open landscapes disappeared due to changing climatic conditions (Hemmer, 1979a).

The initial radiation of the lion apparently followed the explosive Pliocene radiation of the Artiodactyla into the grasslands (Thenius and Hofer, 1960; Maglio, 1975), although the ancestrial form was probably a forest dweller, as suggested by the pelage spots on the young (Bertram, 1978). Similarly, the earlier divergence of the *tigris* line from the *Panthera* stock may have followed the Pliocene radiation of the cervids in southeast Asia (Flerov, 1960; Geist, 1971b), as the evolution of larger bodied forest/grassland ungulates (e.g., *Axis*, *Rusa*, *Cervus*, *Bos*, and *Sus*) probably created a niche for a larger bodied, forest edge predator. If the geographic radiation of the tiger did not take place until the Holocene as Hemmer (1979a) suggests, then their initial radiation may have occurred during the periodic Pleistocene glaciations when sea levels were lower and seasonally drier climates prevailed in southeast Asia (Whitmore, 1975). During these Pleistocene glacial periods, sea levels in southeast Asia fell by as much as 100 m (Haile, 1971) and the entire Sunda Shelf, on which lies Borneo, Java, Sumatra, and Malasia, was connected to the mainland. The disjunct distribution, through portions of India and Sri Lanka of *Leguminosae* (a drought indicating family endemic to the monsoon rain forest of Malasia) implies a greater extend of monsoon climates in the past (van Meewen, Nooteboom, and van Steenis, 1961). The seasonally drier climate (monsoon) that accompanied such glacial periods may have created the patchy grassland/forest conditions that favored the geographic radiation of the cervids and consequently the tiger. Thus, the lion and tiger have been specialized predators for a long time, albeit in somewhat different habitats.

At the present time lions are found in Africa and in India, where they are restricted to a small relict population in the Gir Forest. Until the last century their former range in India and the Middle East was also shared with the cheetah, suggesting that there too they were an open savanna predator, probably living in social groups similar to those found in Africa today.

In contrast, the recent distribution of the tiger extends from the Caspian and Aral Seas across southern Asia to the Sea of Okhotsk and south into India and southeast Asia, some areas of which lions formerly traversed. Their niches are separate, however, the lion adapting to dry open savanna and the tiger to moist forest biotopes.

Though separated for probably a million years the tiger and the lion are strikingly similar morphologically, with the lion retaining essentially the same body proportions as that of a forest field (Gonyea, 1976). Its limb proportions (humeroradial index = 98.3), however, are closer to those of the cheetah (103.3) that that of the tiger (89.8) (Gonyea, 1976), suggesting it is slightly more specialized for a cursorial life. Interestingly, Schaller (1972:242) reports that running was involved in 14% of lion hunts and stalking in 22%, both featured in 88% of all hunts. Nevertheless, both are morphologically adapted for the single-handed capture and killing of prey as large or larger than themselves, a specialization that required only minor morphological change from the primitive felid (Kleiman and Eisenberg, 1973). The skull and dentition patterns of the two species are almost indistinguishable. The tiger is slightly larger than the lion and both show a similar degree of sexual dimorphism. Their gestation period, litter size, tooth replacement patterns, and age of sexual maturity are also nearly identical (Hemmer, 1979b). There do not appear to be major differences in their patterns of olfactory marking (Table 19), and the vocal repertoire of each species is about equal (Schaller, 1967; 1972), although structural differences occur in their vocalizations (Peters, 1978). Both have a large brain and they stand at the top of the felid cephalization, having a mean brain size value of 16 (lion) and 17 (tiger) (Hemmer, 1978b). If brain size is an index of social capacity, then the tiger could be as social as the lion.

The major differences between the tiger and the lion is their degree of sociality. Lions have evolved a complex social unit based on an extended mother-daughter association (Kuhme, 1966; Schenkel, 1966; Schaller, 1972; Bertram, 1978), and the acceptance of allied adult males as part of the unit also indicates the development of greater social tolerance than is seen in other felids. Factors promoting sociality in lions are generally thought to be related to increased efficiency in hunting, feeding, and defending large kills in open habitats, and reduced mortality of young in areas where competitors and/or other predators are common (Schaller, 1972; Caraco and Wolf, 1975; Bertram, 1978; Lamprecht, 1978; Eaton, 1979). However, pride size and intergroup spacing patterns can be quite variable, depending largely on prey density and dispersion. In general, lion social behavior is less well developed than in the canids, as shown in lions by intragroup aggression during communal feeding and periods of food scarcity (Schenkel, 1966; Schaller, 1972; Bertram, 1978). Some regard the latter as indicative of a social organization that has only recently evolved (Schaller and Lowther, 1969; Ewer, 1973; Kleiman and Eisenberg, 1973).

Tigers, by contrast, like most felids, have remained solitary and show a spatially or temporally dispersed social system. In zoos, however, tigers are maintained in pairs or social groups without problems, indicating that the tiger can show greater social tolerance. As previously discussed, the demands of living in dense cover where prey are scattered and time-consuming to locate have apparently not fostered the development of complex social structures. Under these conditions there is no selective advantage for cooperative hunting or feeding and, in fact, the reduction of mutual interference is desirable. While there appears to be pressure on females with small young to avoid situations where other conspecifics may be encountered, the possibility of infanticide, or young being killed by other predators, is most certainly less than that experienced by lionesses in East Africa. Tigresses secrete young in dense cover and restrict their movements to areas around the site until the young are mobile; females with small cubs are also highly aggressive toward intruders. Furthermore, the exclusion of other adult males by the resident provides a form of indirect defense for females in his area.

Their social systems can be regarded as strategies that have evolved through which individual fitness is maximized under various environmental restraints. There are obviously selective advantages to certain behavioral patterns in different habitat types and the adaptive responses to meet the demands of different ecological conditions can be seen in the lion and the tiger–two phylogenetically related, morphologically similar species that specialize in capturing prey as large or larger than themselves.

The lion's habitat in most parts of its range differs significantly from that of the tiger's by (1) being low structured or open; (2) containing an array of prey that often occur in large herds; and (3) supporting a diverse number of serious or influential competitors. Lions have been successful in exploiting this niche by the formation of permanent social units, composed mainly of related females that may hunt and feed together. Although the actual hunting and killing is often accomplished by a single lion, Schaller (1972) reports that hunting success is commonly doubled when several lions are involved. He also points out that by cooperating lions are able to kill larger prey. In this situation, even injured animals can subsist and food is also available for pride members who are protecting or otherwise caring for young.

Aside from the obvious benefits accrued by increased hunting success, one of the important factors favoring sociality appears to be the defense of kills. Hyenas (*Crocuta crocuta*) occur throughout most of the lion's range, are ecologically very similar to the lion, take similar size prey, and aggressively attempt to scavenge lion kills (Kruuk, 1972). Wild dogs (*Lycaon pictus*) have also been known to appropriate lion kills (Guggisberg, 1961), although this is probably not a common occurrence. The combined observations of Schaller (1972) and Kruuk (1972), as summarized by Caraco and Wolf (1975), indicate that if less than four lions utilize a carcass they lose 10% of the meat, whereas four or more lions suffer negligible losses to scavengers. Vultures quickly attract competitors and/or scavengers to kills in open habitats and, whereas a single tiger often feeds on a kill for several days with little interference, a single lion may lose its kill to scavengers in a matter of minutes. Similarly, competition over kills may favor large hunting groups of hyenas (Kruuk, 1972) and wild dogs (Estes and Goddard, 1967). Group size would thus appear to be optimum when it is large enough to defend the kill and utilization (energy returned/energy expended/individual) does not drop below a daily minimum requirement. It has also been shown that lions form larger groups than would be predicted by maximum foraging efficiencies (Caraco and Wolf, 1975), indicating the importance of other constraints such as interference competition on the social system.

Another important factor promoting sociality in lions is reproductive success. Mortality is high in young, but in prides more survive past the age of 2 years than for nomadic lionesses (Schaller, 1972). This increase is largely attributable to protection and feeding by related pride females, who themselves are likely to have young of the same age. Furthermore, lionesses are highly aggressive toward females who are not associated with the pride (Schaller, 1972). Pride males also contribute, principally by providing protection from nomadic males, and by occasionally sharing food and caring for young, a form of direct male parental investment that is uncommon in felids (Kleiman and Malcolm, 1981). Such behavior has not been recorded in tigers, although McDougal (1977) observed an adult male to "wait his turn" before feeding on a bait that had been killed by his presumed subadult son.

Alliance of adult males are also unusual in carnivores, but in lions this appears to operate for the increased success in obtaining and maintaining access to pride females. Intense competition exists between male coalitions for short-term reproductive advantages, and turnover in pride males is relatively frequent, sometimes every two to three years (Schaller, 1972; Bertram, 1978). A male's reproductive success is thus increased when, in collaboration with other males, it is possible to maintain control of a larger pride for an extended period, so that more young are likely to be born and cub mortality is reduced (Bygott, et al., 1979).

In contrast to that of the lion, the tiger's habitat is typically closed, contains relatively fewer and smaller prey that are often scattered, and in most areas serious competitors are absent or occur at low densities. The paucity of competitors is probably linked to the forest habitat, which in tropical areas appears to have favored felid diversity rather than canids (Kleiman and Eisenberg, 1973). Tigers, largely by virtue of their size, are dominant over other felids, and the only potential canid competitor is the wild dog (dhole), a pack-hunting animal. Dholes are sympatric with tigers over much of the latters range, although it is only in the more open habitats of peninsular India that wild dogs appear to be common (Sankhala, 1977). In Chitawan Park, for example, dholes have been observed only once in a 7-year period.

Tigers have been successful in exploiting their niche by remaining solitary. Cooperative hunting, as seen in the lion, would not seem to be beneficial or, under most circumstances, even possible as visual coordination of movement is precluded by dense vegetation and vocalizations would be counterproductive. The rate of detection of prey is probably not increased by incorporating more tigers, and even it it was, and prey were then more easily captured (unlikely), the energy return per individual from the size of prey available would likely be less than that already attainable by a solitary tiger. In the absence of competitors a tiger can utilize each carcass, and thus there is no necessity to share. To efficiently operate as a group tigers would have to increase the rate of prey capture and/or take much larger prey. Large animals such as elephants, rhinos, water buffaloes, gaur, and moose (*Alces alces*) occur in some portions of the tiger's range, the latter being found in the USSR. The first two, by virtue of their size, are essentially invulnerable even to group-hunting lions or hyenas (Schaller, 1972; Kruuk, 1972), and the last three, while occasionally taken by a single animal (Schaller, 1967; Daniel and Grubh, 1966; Sankhala, 1977; Matjushkin, et al., 1977), do not occur at high densities. Thus, under these circumstances, group hunting by tigers would appear to be uneconomical.

The relatively sparse and scattered prey base and attendant hunting and feeding strategies also promotes a temporally or spatially dispersed social system. In Kanha Park for example, the ranges of three tigresses overlapped but each centered its activities in a different area and only rarely were two females seen in one area at the same time (Schaller, 1967). In this study when two or more tigers were found in the same area they were not usually near each other or they visited the area at different times. Indeed, joint use of specific locales could result in interference and reduced hunting success, depending of course on the timing of use and consequent changes in wariness of the prey. Hornocker (1969:463) also speculated that, with respect to mountain lions, the "chances of success in an area already hunted or being hunted by another individual are much less than in an area where prey animals are undisturbed." These same factors appear to influence the manner in which a tiger uses its range, as suggested by frequent changes in daily locations and by the fact that animals did not usually revisit an area during a night of presumed hunting. It was also evident from tracks that tigers rarely retraced their movements, although an animal might follow the same route on consecutive nights.

While a solitary social system is generally considered to be conservative, the more-or-less exclusive home range of tigers has probably been favored by its advantages to both sexes in terms of mating, reproduction and care of young. Males, by excluding other males from their ranges, ensure access to females and maximize their reproductive success by copulating with as many females as possible. For example, male 105 expanded his range when the opportunity arose, and doubled the number of females with which he could potentially mate. A male's reproductive success may also be increased by being familiar to females and with their habits (Zajonc, 1971). No social bond is evident between the sexes although a pair may mate over several reproductive seasons.

The exclusion of other males also reduces potential competition for resources needed by females that are likely to be pregnant, lactating, or have nutritionally dependent young, thereby indirectly contributing to a female's chances of successfully rearing her and his offspring. Differential utilization of habitats, as recorded between the sexes in Chitawan (Table 8), would further reduce competition. The possibility of infanticide is also lessened by the exclusion of other adult males.

Females rear young without direct male involvement, but site attachment, familiarity with the area, and aggression toward intruders likely increases her chances of reproductive success. By restricting their movements to relatively small areas females ensure access to resources that are critical, and fidelity to a site appears strong. Several females in Chitawan are known to have resided in their respective areas for almost eight years (McDougal, pers. comm). Over time the acquired detailed knowledge of an environment probably increases a tiger's hunting success, an important factor for females who must kill regularly and predictably to successfully rear offspring. Avoidance of other tigers, particularly when with small cubs, indicates defense of young is an important aspect of the female's maternal investment. Providing food, training of young, and the possible shifting of females to accommodate their daughters further suggests considerable maternal investment. A female's reproductive fitness may be maximized by choosing to mate with the "best" male, although tigresses (and lionesses) may have no choice, since a male is able to maintain exclusive rights to an area. Presumably this is some measure of his fitness.

Despite differences between lions and tigers in the hunting and feeding strategies and care of young, both species exhibit somewhat similar and flexible responses to variations in prey density, dispersion, and defendability of resources. For example, in the harsh conditions of the Kalahari Desert, where the habitat cannot support a large herbivore biomass, lions commonly exist in small prides (about two to five lions) or they are solitary (Eloff, 1973b). In this area small and/or young mammals make up over 50% of lion skills. Their ranges are large (119–275 km^2), overlap extensively, and lions travel considerable distances during hunting periods, averaging about 11–26 km/day (Eloff, 1973a). Defense of food resources under these conditions would seem to be uneconomical and the sharing of ranges between prides suggests that territoriality, in the sense of an exclusive area, is not rigidly imposed.

By comparison, in areas such as the woodlands of the Serengeti, where there is an abundant resident population of large ungulates, prides "typically" include nine adults plus a varied number of young (Bertram, 1978). The size of pride areas are comparatively small (25–105 km^2), non-overlapping, and lions seldom travel more than about five km/day to secure food. Small mammals form an insignificant part of their diet.

The idea that the distribution and abundance of prey has an effect on lion demography is also evident from two studies in the Serengeti. During Schaller's (1972) study period (1966–1969) few lions remained on the plains during the dry season, but recent studies by Hanby and Bygott (1979) show year-round prides on the plains with increases in pride size and cub survival. These changes coincide with increases in dry-season rainfall and resident prey species.

Such flexibility is also observed in tigers by comparing the land tenure system in Chitawan and the USSR. It is even more evident from changes that have reportedly occurred in Kanha Park. Whereas Schaller (1967) found the home ranges of resident females in Kanha to overlap extensively when he was there, Panwar (1979) reports that in the same area females are now occupying smaller, mutually exclusive ranges. Tiger density does not appear to have increased (Table 5), but improvements in habitat quality has resulted in dramatic increases in the number and distribution of prey species (Coe, 1979). Presumably females are now able to meet their energy and other resource requirements within much smaller areas, and that maintainance of exclusive ranges has become economically feasible. Whether reproductive success has also increased has not been shown.

For both lions and tigers the use of space is a critical factor in gaining access to food, mates, and for rearing offspring. Lions have been successful in competing amongst the open savanna predators, not by morphological specializations per se, but by evolving a complex yet flexible social unit that enables individuals to change from solitary to social hunters while maintaining the benefits of the pride. Under adverse conditions, however, intra-group competition becomes intense and cubs may starve, juveniles and lionesses may be killed, and a general intolerance of conspecifics is evident (Schenkel, 1966; Schaller, 1972; Bertram, 1978).

Tigers, by contrast, have been successful by remaining solitary, cryptic, and dispersed. They are capable of socializing, as gatherings at large and steady food sources indicate, and little overt aggression is seen in these situations or in captivity, suggesting the potential for development of a social unit based on increased tolerance of conspecifics. The possibility of home range inheritance by female offspring, as noted in Chitawan (this study) and Kanha Park (Panwar, 1979), raises additional implications for the evolution of some type (deme) of sociality in tigers. Indeed, in a long-term study it may emerge that two or more females sharing a range are related.

Summary

As part of a long-term study of the ecology of the tiger the movements and socio-spatial system was investigated using radio-telemetry. The response of individuals to capture, handling, radio-tagging, and subsequent tracking did not suggest that they were disturbed by the process.

The number of resident tigers in the park appears to be stable, with an adult sex ratio (1 : 4) favoring females. The crude density of adults is one per 36 km^2 but in areas of prime habitat is considerably higher. While the number of dependent and independent offspring can vary considerably, most resident females were either pregnant or with dependent young during the study period. More young are reaching maturity than there are available vacancies, thus the park serves as a reproductive nucleus for the surrounding area. Reproductive activity appears to be high in the cool season and early part of the hot season, although young may be born at any time of the year. Females that lose a litter are capable of having young again within several months, but if the young survive a female produces a litter about every two to two and a half years. Most females are not seen with more than three young. Estrus is apparently suspended until the young have reached independence, at about 18 months old. Mortality in young, especially in the first two years of life, may be as high as 50% and is related to many factors.

Tigers were primarily nocturnal but some daytime activity and movement was not uncommon. Activity patterns varied seasonally, apparently in response to changes in the activity schedules of the prey, ambient temperatures, and energy requirements. There was no significant seasonal difference between males and females in the amount of daytime activity. Leopards in the same area were significantly less active than tigers, both during the day and at night, which is probably related to avoidance of tigers.

Riverine forest and grassland habitat types are preferred by tigers over sal forest. Conditions in these types are more favorable for hunting success, almost 90% of tiger kills were found in riverine forest/grassland. Seasonally, differences in the utilization of habitats varied with components such as the distribution and availability (vulnerability) of prey, cover, and water. In addition, males and females showed significant seasonal differences in habitat use, which may represent an adaptation to reduce conflict for resources.

Tigers are highly mobile animals, frequently changing locations, and infrequently reusing specific rest sites. Such a pattern is obviously related in part to finding food, as departures from this movement pattern were usually (90% of time) associated with a kill. While the linear distance between consecutive locations averaged 2.0 km, tigers travelled an estimated 10–20 km/day. An adult male travelled significantly farther between daily locations than females or subadults; he visited most parts of his range relatively frequently (three to four times/month), stayed a short time (one to two days), and returned at fairly short intervals (five to seven days). This movement pattern probably ensures that a male detects any estrous females as well as intruders. Females visited most parts of their ranges at intervals of a few days to two weeks. The birth of young and their gradual maturation has a marked localizing effect on the movements of females.

The home ranges of tigers were well delineated, stable for several years, and were only appropriated by other adults in response to the resident's death or through lack of use. Males occupied large, mutually exclusive ranges that encompassed those of several females, which also were exclusive, suggesting their ranges were also territories. Ranges varied in size from 60–72 km^2 (adult males) to 16–20 km^2 (adult females). Seasonally, home ranges tended to be smallest in the wet season. Occupancy apparently confers rights to an area, as no transient or resident settled permanently in an occupied range. Maintainance of home ranges and the social interactions within them were probably promoted by various sensory modalities, including olfactory, visual, and auditory signals, acting alone or in concert; overt interactions were not recorded during the study.

Adult and independent subadult tigers were found to socialize infrequently. Even among animals sharing a range they were commonly two to five km apart. Tigers are capable of socializing, as observations at kills indicate, but the only prolonged contact is between mother and young. Females with small cubs did not associate with adult males, in fact, adults of the opposite sex were located together on few occasions outside of periods of suspected sexual activity. The latter was suggested by vocalizations, changes in scent-marking behavior, and association with an adult male.

Data on killing techniques indicate that when the weight of the prey is more than half that of the tiger it uses a throat bite to kill. Most of the prey killed by tigers weighed 50–100 kg, but animals weighing 400 kg were also taken. Leopards in the same area took smaller prey, most of which were in the 25–50 kg range. Wild ungulates, principally deer, occurred in 85% of tiger feces and 64% of kills; this difference is related to more domestic livestock in the kill data and a clumped distribution of livestock kills. Sambar are preferred prey and/or they are more vulnerable. Tigers killed animals over a broad range of age classes, including young, old, and prime adults, suggesting that their hunting methods take more of a random sample of the population than does coursing. Tigresses without dependent young made a kill about every 8–8.5 days or 40–50 kills/yr. The average length of time spent with kills was three days, during which a tiger consumed an averaged of 46 kg. On a yearly basis tigresses ate 5–6 kg/day; for males the amount is probably 6–7 kg/day.

An assessment of the impact of predation on prey populations indicated tigers are removing about 8%–10% of the available wild ungulate biomass, but with the exception of sambar, prey species do not appear to be limited by predation.

Results from this study are then viewed in an evolutionary perspective in comparison with the lion, a phylogenetically related, morphologically similar species, that shows a greater degree of sociality.

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